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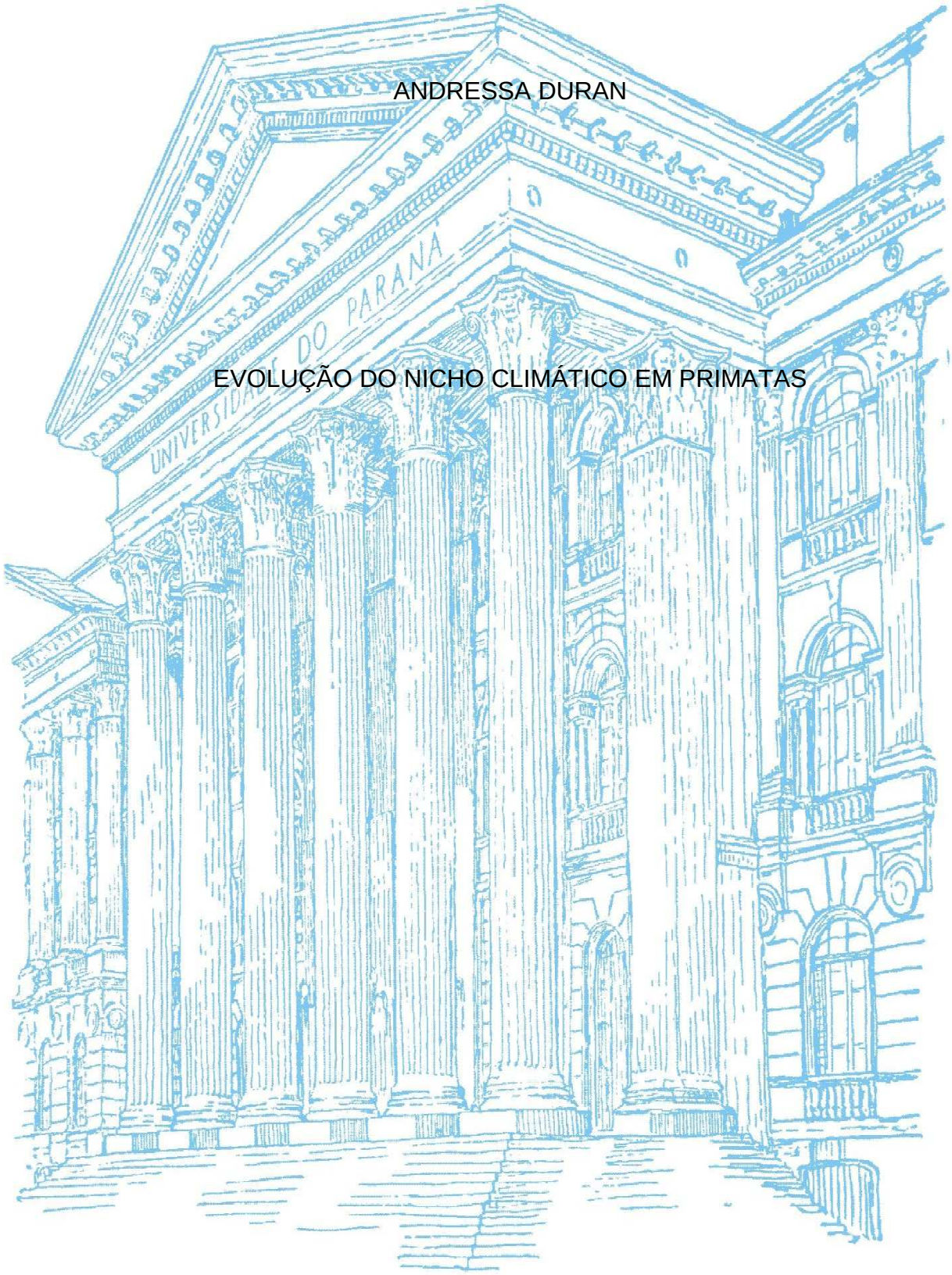

EVOLUÇÃO DO NICHO CLIMÁTICO EM PRIMATAS

CURITIBA
2016

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Dissertação apresentada ao Programa de Pós-Graduação em Ecologia e Conservação do Setor de Ciências Biológicas da Universidade Federal do Paraná, como requisito parcial para obtenção do título de Mestre em Ecologia e Conservação.

Orientador: Prof. Dr. Marcio R. Pie

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PARECER

Os abaixo-assinados, membros da banca examinadora da defesa da dissertação de mestrado, a que se submeteu **Andressa Duran** para fins de adquirir o título de Mestre em Ecologia e Conservação, são de parecer favorável à **APROVAÇÃO** do trabalho de conclusão da candidata.

Secretaria do Programa de Pós-Graduação em Ecologia e Conservação.

Curitiba, 25 de fevereiro de 2016.

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"Love many things, for therein lies the true strength,
and whosoever loves much performs much,
and can accomplish much,
and what is done in love is done well."

Vincent Van Gogh

RESUMO

O estudo dos nichos climáticos, segundo seu *tempo* e *modo* de evolução, podem fornecer informações valiosas sobre os padrões e processos envolvidos na diversificação das espécies. Apesar do grande interesse na dinâmica de nicho pelos estudos macroecológicos, a compreensão sobre como os nichos climáticos mudam ao longo do tempo evolutivo está apenas em seu início. A disponibilidade de informações sobre características das espécies e sobre suas histórias evolutivas, assim como o desenvolvimento de abordagens filogenéticas comparativas modernas, mudou consideravelmente ao longo dos últimos anos. Com base nestes conjuntos de dados abrangentes e no desenvolvimento metodológico, torna-se, portanto, oportuno decifrar os aspectos fundamentais à respeito da evolução dos nichos climáticos. Neste estudo foram integrados informações sobre a distribuição geográfica das espécies, suas preferências climáticas e a relação filogenética entre 334 espécies de primatas, com o objetivo de compreender a evolução dos nichos climáticos ao longo do tempo e entre as principais linhagens de primatas: Strepsirrhini, Catarrhini e Platyrrhini. O espaço de nicho climático para cada espécie foi caracterizado utilizando a análise de componentes principais (PCA), e os três primeiros PCs foram selecionados, somando a maior parte da variação no conjunto de dados. Em seguida, o PC1, associado com condições climáticas frias, o PC2, associado com condições quentes e secas, e o PC3, relacionado com climas quentes e úmidos, foram submetidos à análises que avaliaram a adequabilidade dos modelos de evolução. Além disso, a evolução dos caracteres também foi avaliada utilizando métodos que permitiram a identificação do número, localização e direção de mudanças nas taxas de evolução. Estas análises indicaram que a evolução do nicho climático em primatas é caracterizada por uma considerável heterotaquia, e portanto, modelos simples de evolução fornecem uma representação inadequada sobre como os nichos evoluem. Todos os clados apresentaram mudanças recentes nas taxas de evolução de nicho climático, particularmente ao longo dos últimos 10 milhões de anos, e estes eventos foram associados com as mudanças climáticas na temperatura global que ocorreram durante a diversificação de espécies de primatas.

Palavras-chave: Catarrhini, Heterogeneidade de taxas, Mudança climática, Macroecologia, Métodos filogenéticos comparativos, Mioceno, Platyrrhini, Strepsirrhini.

ABSTRACT

The study of climatic niches, according to their tempo and mode of evolution, can provide powerful insights into the patterns and processes shaping species diversification. Despite the extensive interest in niche dynamics by macroecological studies, the understanding of how climatic niches change over the evolutionary time it is only in its beginning. The availability trait species information and their evolutionary history, as well as the development of modern phylogenetic comparative approaches, changed considerably in the last few years. Based on such comprehensive datasets and methodological framework, it is, therefore, timely to decipher key aspects regarding climatic niche evolution. In this study were integrated species geographical distribution information, their preferable climatic conditions, and the phylogenetic relationship among 334 primate species aiming to understand the evolution of climatic niches through time and among the main primate lineages: Strepsirrhini, Catarrhini, and Platyrrhini. The climatic niche space for each species was characterized by a principal component analysis (PCA), and the first three PCs, which accounted for the majority of the variance in the dataset, were selected. Then, the PC1, associated with colder climatic conditions, the PC2, associated with warmest and drier conditions, and the PC3, related to warmest and wettest climates, were subject to analyses that evaluated the adequacy of models of evolution. Additionally, trait evolution was also accessed using methods that allowed the identification of the number, location, and direction of shifts in rates of evolution. These analyses revealed that primate climatic niche evolution is characterized by considerable rate heterogeneity, and therefore, simplistic evolutionary models provide a poor representation of how climatic niches evolve. All clades presented recent changes in rates of climatic niche evolution, particularly over the last 10 My, and these events were linked to climate changes in global temperature during the primate species diversification.

Keywords: Catarrhini, Climate change, Macroecology, Miocene, Platyrrhini, Phylogenetic comparative approach, Rate heterogeneity, Strepsirrhini.

SUMÁRIO

INTRODUÇÃO GERAL

O conceito de nicho

O nicho é um dos pilares do pensamento ecológico (BROWN 1995, CHASE; LEIBOLD 2003, GIBSON-REINEMER 2015). É um importante conceito para integrar fenômenos ecológicos e evolutivos, uma vez que é capaz de abranger diversos níveis de organização (populações, espécies) e escalas (CHASE; LEIBOLD 2003, WAKE *et al.,* 2009). Esta abrangência fez com que o nicho tenha se tornado parte fundamental de diversas disciplinas atuais, como Ecologia Evolutiva (PIANKA 1994), Macroecologia (WIENS *et al.*, 2010, DINIZ-FILHO *et al.*, 2013), Biogeografia (WIENS; DONOGHUE 2004, WIENS; GRAHAM 2005) e Biologia da Conservação (PETERSON 2003, WIENS *et al.*, 2009, PETERSON *et al.*, 2011), tendo inclusive sido descrito recentemente como uma questão prioritária em estudos Paleoecológicos (SEDDON *et al.*, 2014).

A história do conceito de nicho teve sua origem no início do século XX. A utilização da palavra nicho pela primeira vez na Ecologia é atribuída à Roswell Johnson (1910), que a definiu como o espaço da espécie no ambiente. Entretanto, a palavra nicho só começou a ganhar sua conotação científica quando Joseph Grinnell, em 1917, usou o termo de maneira explícita. Sua definição estava baseada na análise das condições ambientais presentes na área de distribuição geográfica da espécie *Toxostoma redivivum* (Passeriformes, Mimidae), que possuía uma distribuição bastante restrita quando comparada com outras espécies de aves. Esta restrição foi associada fortemente às características específicas de nicho da espécie. Segundo a ideia de Grinnell, o nicho seria uma propriedade do ambiente (GRINNELL 1917, 1924). Em 1927, outra definição de nicho foi elaborada independentemente pelo ecólogo Charles Elton, que observando as relações interespecíficas destacou que a presença de uma espécies estaria fortemente associada com a presença de outras espécies no mesmo local. Elton definiu o nicho como o papel funcional da espécie no ambiente, enfatizando as relações do tipo predador-presa. Curiosamente, anos mais tarde a definição de Elton foi utilizada como uma das bases para a elaboração do princípio da exclusão competitiva de Gause (GRIESEMER 1994). Outros conceitos de nicho menos explorados são de Dice (1952), Clarke (1954) e Weatherley (1963; PIANKA 1994).

O conceito moderno de nicho foi desenvolvido em 1957, por George Evelyn Hutchinson. Este conceito elegante e elaborado teve grande impacto no pensamento ecológico (GRIESEMER 1994), definindo o nicho de maneira mais formal e utilizando elementos dos dois conceitos para construir uma ideia de nicho multidimensional. Para Hutchinson, o nicho da espécie engloba tanto as variáveis bióticas quanto as abióticas, ou seja, um total de condições e recursos sob os quais os organismos vivem e se mantêm indefinidamente (HUTCHINSON 1957). O nicho Hutchinsoniano é descrito como um hipervolume n-dimensional. Graficamente, cada uma das variáveis ambientais (que devem ser independentes) representa um eixo, logo, quanto mais variáveis forem consideradas para descrever o nicho da espécie, mais dimensões serão acrescentadas ao gráfico. Isto aumenta sua complexidade, o que torna o conceito abstrato e difícil de ser aplicado na prática (PIANKA 1994). Hutchinson separou o conceito em nicho fundamental e realizado (HUTCHINSON 1957, 1978). O nicho fundamental reúne todos os fatores sob as quais os organismos conseguem persistir, onde o ambiente físico é ótimo, excluindo qualquer interação com outras espécies. É, portanto, um ambiente hipotético e idealizado. Os componentes do nicho fundamental foram divididos em variáveis scenopoéticas e bionômicas, representando respectivamente as condições (e.g. temperatura e precipitação) e recursos (variáveis que promovem competição; e.g. alimento) necessários para a espécie (HUTCHINSON 1978). O nicho fundamental pode ser traduzido no espaço geográfico/ambiental como nicho realizado, que reúne as reais condições requeridas pela espécie, e inclui interações negativas entre as espécies (Hutchinson considerou apenas a competição). O nicho realizado terá, portanto, amplitude menor (subconjunto) ou igual ao nicho fundamental, sendo descrito como o nicho real da espécie (HUTCHINSON 1978). Esta subdivisão dos nichos é amplamente utilizada, particularmente em estudos de modelagem de distribuição de espécies (SOBERÓN; PETERSON 2005, PETERSON *et al.,* 2011). Entretanto, as ideias de nicho fundamental e realizado são frequentemente utilizadas imprecisamente, com a mesma ideia representando conceitos diferentes, dependendo do estudo (PIANKA 1994, CHASE; LEIBOLD 2003, ARAÚJO; GUISAN 2006, e.g. GUISAN; ZIMMERMANN 2000, SOBERÓN; PETERSON 2005). Soberón (2007) sugeriu que as variáveis scenopoéticas poderiam ser interpretadas como nicho Grinnelliano, enquanto as variáveis bionômicas seriam o nicho Eltoniano. Essa

separação possibilitou o esclarecimento dos conceitos e tem sido frequentemente utilizada, mesmo que implicitamente (e.g. GUISAN; ZIMMERMANN 2000, COOPER *et al.,* 2011, GOUVEIA *et al.*, 2013, DURAN *et al.,* 2013, DURAN; PIE 2015).

Nicho climático

A distribuição geográfica das espécies é governada por diversos fatores, como a capacidade de dispersão das espécies, as interações biológicas e as condições ambientais (WIENS; DONOGHUE 2004, BEHRENSMEYER 2006, FUTUYMA 2009, GOUVEIA *et al.*, 2014). Dentre esses fatores, o clima é reconhecidamente um fator determinante, sendo capaz de explicar grande parte dos padrões espaciais de distribuição das espécies (ELTON 2007, DINIZ-FILHO *et al.,* 2009), uma vez que a espécie não poderá ocorrer fora dos seus limites de tolerância climática (WOODWARD; KELLY 2003, FISHER-REID *et al.,* 2012). Uma maneira informativa de estudar as preferências climáticas das espécies é utilizando o conceito de nicho climático, que é um aspecto do nicho ecológico, sendo definido como o conjunto de condições climáticas associadas à distribuição das espécies (nicho Grinnelliano - SOBERÓN, 2007).

A evolução dos organismos ocorreu em um planeta altamente dinâmico, com oscilações climáticas de todas as magnitudes, desde variações modestas de temperatura até ciclos extremos glaciais-interglaciais, como por exemplo as intensas mudanças climáticas no Cenozóico (JANIS 1993, VRBA 1995, ZACHOS *et al.,* 2001, JABLONSKI *et al.,* 2003, CLARKE; CRAME 2003). Portanto, os aspectos climáticos que são importantes para uma espécie dependem da trajetória dela ao longo da sua história evolutiva (FUTUYMA 2009). Sendo assim, os nichos climáticos das espécies são dinâmicos, capazes de evoluir ao longo do tempo e no espaço, em escalas ecológicas e evolutivas (PIANKA 1994, PEARMAN *et al.,* 2008).

Tempo e Modo de evolução

O estudo da dinâmica de nicho tem consequências fundamentais para padrões e processos ecológicos (e.g. padrões de riqueza das espécies) e evolutivos (e.g. adaptação das espécies num contexto de mudanças ambientais; PIANKA 1994, PEARMAN *et al.,* 2008, WIENS *et al.,* 2010, PETERSON *et al.,* 2011). Uma abordagem interessante para avaliar como os nichos climáticos mudam ao longo da

história é investigar o *tempo* e o *modo* de sua evolução. George Gaylord Simpson (1944) definiu o termo *tempo* referindo-se às taxas de evolução, enquanto o *modo* seria a maneira como a evolução ocorre, tendo o *tempo* como um elemento fundamental, mas envolve mais do que apenas as taxas. De uma maneira mais direta, o *tempo* pode ser interpretado como um padrão e o *modo* como um processo, e assim o *modo* pode ser inferido através do *tempo* (GOULD 1994; HUNT 2012).

O estudo das taxas de evolução tem um papel importante na Biologia Evolutiva (DINIZ-FILHO 2000), sendo reconhecido há muito tempo que as taxas de evolução mudam ao longo da história dos clados, e podem, por exemplo, ser rápidas ou lentas (SIMPSON 1944, 1953). O *modo* de evolução dos nichos pode ser avaliado utilizando modelos evolutivos (e.g. movimento Browniano (FELSENSTEIN 1973, 1985), Ornstein-Uhlenbeck (HANSEN 1997), *Early Burst* (BLOMBERG *et al.,* 2003; HARMON *et al.,* 201)), que podem ser analogamente comparados com regras determinadas. Ao longo do processo evolutivo de uma linhagem, os caracteres mudariam de acordo com essas regras (DINIZ-FILHO 2000). Desta forma, o estudo do *tempo* e *modo* de evolução do nicho possibilita a identificação de mudanças nas taxas evolutivas, permitindo criar hipóteses sobre os processos relacionados com tais mudanças.

Adequabilidade dos modelos evolutivos e Heterogeneidade

Identificar o modelo de evolução de melhor ajuste aos dados é importante para fazer inferências à respeito da evolução dos caracteres (REVELL *et al.,* 2008, PENNELL *et al.,* 2015). Contudo, para fazer qualquer inferência sobre o modelo de evolução é fundamental avaliar se o modelo está realmente explicando a variação existente no conjunto de dados (PENNELL *et al.,* 2015). Muitos modelos evolutivos foram descritos com base em taxas globais de evolução (uma única taxa de evolução para todas as espécies da filogenia), e variam quanto ao processo evolutivo considerado, com a mudança do caráter podendo ser descrita, por exemplo, através de flutuações aleatórias ou através de seleção direcional (FELSENSTEIN 1985, HANSEN 1997, THOMAS *et al.,* 2015). Estes modelos são frequentemente utilizados para descrever a evolução de caracteres morfológicos (e.g. COOPER; PURVIS 2010), de nichos ambientais (e.g. KAMILAR; MULDOON 2010, LITSIOS *et al.,* 2012, DURAN *et al.,* 2013), de comportamento e história de

vida (e.g. SMITH; BEALIEU 2009, KAMILAR; COOPER 2013). Entretanto, existe uma forte discussão sobre as incertezas quanto ao ajuste destes modelos, particularmente à respeito do tamanho do conjunto de dados utilizado e possíveis tendências de ajuste de um modelo (geralmente Ornstein-Uhlenbeck) em relação aos outros (e.g. BOETTIGER *et al.,* 2012, PENNELL *et al.,* 2015, SILVESTRO *et al.,* 2015, THOMAS *et al.,* 2015). Questiona-se ainda a relevância destes modelos simples de evolução para representar os processos evolutivos naturais responsáveis pela evolução dos caracteres (FRECKLETON; PAGEL; HARVEY 2003).

Diferentes intensidades de seleção podem deixar marcas nas taxas e consequentemente nos *modos* de evolução (BAKER *et al.,* 2015). A evolução fenotípica não é caracterizada por taxas homogêneas e isso é reconhecido há algum tempo, porém apenas recentemente evidências começaram a surgir com o desenvolvimento de metodologias que permitiram acessar essa heterogeneidade de taxas evolutivas na evolução dos caracteres (O'MEARA *et al.,* 2006, EASTMAN *et al.,* 2011, REVELL *et al.,* 2011, THOMAS; FRECKLETON 2012, INGRAM; MAHLER 2013, UYEDA; HARMON 2014, KHABBAZIAN *et al.,* 2016). Smith e Beaulieu (2009) demonstraram a existência desta heterogeneidade avaliando que as mudanças na evolução dos nichos climáticos de angiospermas estão relacionadas com o seu tipo de crescimento, com plantas herbáceas tendo taxas de evolução mais rápidas que plantas lenhosas. Price *et al.* (2012) verificou que variações nas taxas de evolução de caracteres morfológicos tróficos e de locomoção de peixes estão relacionados com o ambiente onde eles vivem, mostrando que a evolução destes caracteres são mais rápidos em peixes de ambientes recifais, quando comparados com peixes não recifais. Embora estes exemplos tenham demonstrado de maneira eficiente a heterogeneidade na evolução de caracteres, ambos utilizaram hipóteses determinadas *a priori* para testar mudanças nas taxas de evolução. A abordagem denominada BROWNIE (O'MEARA *et al.,* 2006), utilizada por ambos os estudos mencionados acima, necessita de hipóteses *a priori*, e permite identificar diferentes taxas na evolução de um caráter e assim, avaliar se uma ou múltiplas taxas de evolução se ajustam melhor aos dados. Entretanto, a determinação de hipóteses *a priori* nem sempre é possível e para esses casos não existe uma maneira de determinar quantas mudanças de taxa evolutiva ocorreram ao longo do tempo ou entre as linhagens em uma filogenia (BAKER *et al.,* 2015). A detecção automática de

mudanças de taxas de evolução representou um importante avanço nos estudos comparativos recentes, identificando além do número de mudanças nas taxas, a localização delas na filogenia e a direção dessas mudanças (e.g. EASTMAN *et al.,* 2011, THOMAS; FRECKLETON 2012, VENDITTI *et al.,* 2014, RABOSKY 2014). Essa metodologia têm ganhado destaque no estudo da evolução de caracteres, e a utilização desta abordagem para avaliar a evolução nos nichos climáticos é inovadora, capaz de fornecer indícios sobre os diferentes cenários evolutivos que ocorreram durante a diversificação dos clados, além de permitir uma inferência mais robusta para a estimativa de taxas de evolução.

Primatas como modelo de estudo

Os primatas representam um grupo de destaque para estudos comparativos, uma vez que informações sobre a história evolutiva, suas preferências climáticas e as distribuições geográficas das espécies são melhores compreendidas do que para a maioria dos outros táxons (LEHMAN; FLEAGLE 2006). Os primatas possuem filogenias bastante abrangentes (SPRINGER *et al.,* 2012), fundamentais para este tipo de estudo, uma vez que os padrões filogenéticos das espécies contém em si a assinatura dos processos evolutivos que os geraram (FRECKLETON *et al.,* 2003). Existem aproximadamente 479 espécies de primatas descritas atualmente (MITTERMEIER *et al.,* 2013), com representantes ocupando uma grande amplitude de condições climáticas, presentes nas regiões tropicais e subtropicais. A ordem Primates pode ser subdividida em três grandes clados: a subordem Strepsirrhini e as infraordens Catarrhini e Platyrrhini. Os strepsirrhines, representados principalmente pelos lemuriformes, estão distribuídos geograficamente pela Ásia e África, tendo a maioria de seus representantes concentrados na ilha de Madagascar. Os catarrhines, ou primatas do Velho Mundo, como gorilas, pongos e chimpanzés, estão distribuídos pela África e Ásia (MITTERMEIER *et al.,* 2013), e compreendem espécies presentes nas latitudes mais setentrionais já descritas para primatas (*Rhinopithecus avunculus*, na China, e *Macaca fuscata*, no Japão; WILLIAMS 2016). Os platyrrhines, representados pelos saguis, micos e bugios, possuem distribuição geográfica restrita às Américas Central e do Sul, sendo conhecidos também como primatas do Novo Mundo (GROVES 2005, MITTERMEIER *et al.,* 2013).

Objetivos

Integrar dados de distribuição geográfica, variáveis climáticas e métodos filogenéticos comparativos para avaliar o *tempo* e *modo* da evolução de nicho climático em primatas, observando como as taxas de evolução mudaram ao longo do tempo evolutivo e entre as linhagens. Especificamente, buscou-se determinar os locais de mudanças nas taxas de evolução, tanto ao longo da história evolutiva quanto geograficamente, buscando investigar sobre a ocupação dos nichos das espécies deste grupo e os fatores que causaram os padrões de distribuição geográfica observados atualmente.

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ARTIGO: "Tempo and mode of climatic niche evolution in Primates"

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Tempo and mode of climatic niche evolution in Primates

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Abstract

Climatic niches have increasingly become a nexus in our understanding of a variety of ecological and evolutionary phenomena, from species distributions to latitudinal diversity gradients. Despite the increasing availability of comprehensive datasets on species ranges, phylogenetic histories, and georeferenced environmental conditions, studies on the evolution of climate niches have only begun to understand how niches evolve over evolutionary timescales. Here, using primates as a model system, we integrate recently developed phylogenetic comparative methods, species distribution patterns and climatic data to explore primate climatic niche evolution, both among clades and over time. In general, we found that simple, constant-rate models provide a poor representation of how climatic niches evolve. For instance, there have been shifts in the rate of climatic niche evolution in several independent clades, particularly in response to the increasingly cooler climates of the past 10 My. Interestingly, rate accelerations greatly outnumbered rate decelerations. These results highlight the importance of considering more realistic evolutionary models that allow for the detection of heterogeneity in the tempo and mode of climatic niche evolution, as well as to infer possible constraining factors for species distributions in geographical space.

Introduction

Climatic niches - the set of environmental conditions associated with the occurrence of a given species(Grinnellian niche - Soberón 2007)- has become a central concept in ecology and biogeography in recent years (Pearman et al. 2008; Wiens et al. 2010). For instance, although current patterns of species distributions are ultimately determined by three main mechanisms, namely speciation, extinction, and dispersal (Ricklefs 1987; Wiens and Donoghue 2004; Mittelbach et al. 2007), each of these mechanisms can in turn be strongly affected by climatic conditions, such as temperature and precipitation (Woodward and Kelly 2003; Fleagle and Gilbert 2006; Hua and Wiens 2013; see also Hawkins et al. 2003; Currie et al. 2004; Lomolino et al. 2010; Gavilanez and Stevens 2012; Pyron and Wiens 2013; Smith 2013). This has led to several studies describing the general properties of climatic niches in a variety of taxa (e.g. Hof et al. 2010; Jakob et al. 2010; Kamilar and Muldoon 2010; Cooper et al. 2011; Olalla-Tárraga et al. 2011; Araújo et al. 2013; Bonetti and Wiens 2014). However, our understanding of the tempo and mode of evolution (Simpson 1944) in the case of climatic niches is still incipient, particularly using comprehensive interspecific datasets.

Studies to date on the evolution of climatic niches have primarily focused on two main areas: assessing phylogenetic signal and niche conservatism (e.g. Peterson et al. 1999; Losos 2008; Wiens 2008; Revell et al. 2008; Crisp et al. 2009; Hof et al. 2010; Buckley et al. 2010; Dormann et al. 2010; Wiens et al. 2010; Cooper et al. 2011; Ollala-Tárraga et al. 2011; Peterson 2011; DeSantis et al. 2012; Münkemüller et al. 2012, 2015; Duran et al. 2013; Kamilar and Cooper 2013) and measuring the relative fit of simple

models of trait evolution, such as Brownian motion (BM, Felsenstein 1973, 1985) and Ornstein-Uhlenbeck (OU, Hansen 1997). The latter application has been instrumental to uncover several important aspects of niche evolution, such as its relation to species diversification (Kozak and Wiens 2010a,b; Schnitzler et al. 2012; Machac et al. 2013; Lawson and Weir 2014), the conditions favoring niche divergence (e.g. Evans et al. 2009; Kozak and Wiens 2010a), and the extent to which different climatic niche axes might evolve according to distinct dynamics (e.g. Kamilar and Muldoon 2010; Cooper et al. 2011; Duran et al. 2013). However, there has been increasing concern over whether such simple, time-homogeneous models of trait evolution are able to properly describe trait evolution along actual phylogenetic histories (Freckleton and Harvey 2006; Eastman et al. 2011; O'Meara 2012; Thomas and Freckleton 2011; Pennell et al. 2015). Indeed, the most likely model amongst a set of poor models is still a poor model, and the extent of misspecification in commonly applied models of trait evolution is still poorly known. Alternatives to time-homogeneous models involve the possibility of testing for shifts in the rates of trait evolution, both over time [Early-burst (EB), Harmon et al. 2010; delta, Pagel 1999] and among clades (O'Meara et al. 2006; Thomas et al. 2006; Revell et al. 2011). A common limitation of some models that allow for shifts in rates of evolution in different parts of a tree is the need to specify beforehand the position of such shifts (O'Meara 2012). This limitation has been mitigated by methods that allowed for *a posteriori* location of rate shifts, such as Accommodating Uncertainty in Trait Evolution Using R (AUTEUR, Eastman et al. 2011, see also Venditti et al. 2011) and Models of Trait Macroevolution on Trees (MOTMOT, Thomas and Freckleton 2011) (see also Revell et al. 2011; Ingram and Mahler 2013, and

Uyeda and Harmon 2014 for additional alternatives). Both methods have been used in several studies looking at variation in the evolution of morphological traits (e.g. Anderson et al. 2013; Davies et al. 2013; Garcia-Porta and Ord 2013; Pie and Tschá 2013; Rabosky et al. 2013), yet similar studies on other types of characters, such as climatic niches, are still scarce (but see Smith and Beaulieu 2009 and Litsios et al 2012).

In this study, we combined information on the phylogenetic relationships, climatic data, and phylogenetic comparative methods to provide the most comprehensive study of climatic niches to date. We used the order Primates as our model system, given that they are unparalleled among most taxa with respect to the level of detail in the knowledge about their distribution and phylogenetic relationships (Lehman and Fleagle 2006; Springer et al. 2012). First, we used Principal Component Analysis (PCA) to determine the main axes of variation in climatic niches of 334 primate species. The absolute fit of scores on different principal components (PCs) to several simple models of trait evolution was assessed using posterior predictive simulation, which showed strong evidence for heterogeneity in rates of climatic niche evolution. Such heterogeneity was further explored using methods that quantified variation in rates both over time and among lineages. In particular, our results indicate several independent shifts in rates of climatic niche evolution, especially over the past 10 My, possibly in association with the period of climatic cooling that took place during the late Miocene.

Methods

Data collection

In order to characterize the evolution of primate climatic niches, we compiled an extensive dataset that included all species for which we could simultaneously obtain information on phylogenetic, distribution, and climatic data. Phylogenetic relationships and divergence times among primate species were obtained from Springer et al. (2012), which is the most complete primate molecular phylogeny to date. Shapefiles of distribution maps were downloaded from the International Union for Conservation of Nature database (IUCN 2012), from which only shapefiles from extant and probably extant species in their native range were retained for later analysis. The final dataset comprised 334 species and included the suborder Strepsirrhini (105 species) and the infraorders Catarrhini (138 species), and Platyrrhini (91 species), representing around 70% of the currently recognized primate species (Mittermeier et al. 2013).

The climatic niche of each species was characterized using data on temperature, precipitation and altitude obtained from WORLDCLIM 1.4 (Hijmans et al. 2005). This dataset consists of 19 bioclimatic variables and altitude, with a spatial resolution of 2.5' (≈5 km). The mean values for each variable across the entire range of each species were obtained and manipulated using the packages RASTER 2.2-31 (Hijmans 2014), RGDAL 0.9-1 (Bivand et al. 2014), MAPTOOLS 0.8-30 (Bivand and Lewin-Koh 2014), and PLYR 1.8.1 (Wickham 2014). All analyses in this study were carried out in R 3.0.3 (R Development Core Team 2014). The final dataset with all studied species and their respective

mean values from each of the 20 variables is available as supplementary material (Table S1).

Data analysis

Raw data were first transformed into *z*-scores and then subject to a Principal Component Analysis (PCA) based on their covariance matrix. We transformed the original data into *z*-scores prior to the PCA given that the vast differences in measurement scales between temperature and precipitation could severely bias the obtained results. This type of approach has been a common practice in studies on the evolution of climatic niches to deal with multicollinearity and to reduce the dimensionality in the studied datasets (e.g. Broennimann et al. 2007; Kamilar and Muldoon 2010; Kozak and Wiens 2010a; Duran et al. 2013). However, it has been recently shown that fitting models of evolution to PCA scores might lead to an artefactual support for reconstructing more variation early in the history of a clade (Uyeda et al. 2015). We addressed this issue by repeating our analyses using a version of the PCA that takes into account the phylogenetic structure of the data when computing the PCA (Revell 2009), as implemented in PHYTOOLS 0.4-45 (Revell 2012). However, given that the PC scores and loadings from both analyses were highly correlated ($r > 0.98$), the results of the phylogenetically-corrected PCA will not be shown for the sake of brevity. The PCA axes retained for later analysis were selected according to the broken-stick criterion (Jackson 1993) using VEGAN 2.0-10 (Oksanen et al. 2013). As a first approximation, to investigate the evolution along each climatic niche axis, we fit three alternative models of evolution to the scores from each of the selected PC axes: (1) the Brownian motion model (BM),

167 in which traits evolve as a random walk process where the trait change follows
168 a constant rate and is non-directional and their magnitude is independent of
169 current or past states through time (Felsenstein 1985); (2) Ornstein-Uhlenbeck
170 model (OU), which tests the scenario of stabilizing selection with a single
171 adaptive peak (Hansen 1997; Butler and King 2004); and (3) the Early Burst
172 model (EB), in which the rate of trait evolution can be accelerated during the
173 early stages of the history of a given clade (Blomberg et al. 2003; Harmon et al.
174 2010). Model fit using the Akaike Information Criterion (AIC, Akaike 1973) were
175 calculated using GEIGER 2.0.3 (Pennell et al. 2014a).

176 The level of adequacy of the tested models was assessed using
177 posterior predictive simulation (also known as parametric bootstrapping), as
178 implemented in ARBUTUS 1.1 (Pennell et al. 2014b). In brief, the best-fit model,
179 as indicated by the lowest AIC value in previous analyses, was matched with
180 the trait data and used to create a unit tree. This unit tree is a transformation of
181 the original phylogenetic tree, which is molded to capture the evolutionary
182 dynamics with which a particular trait evolves according to the selected model.
183 Based on this unit tree, we simulated 10000 datasets using the estimated
184 parameters. A series of test statistics were then calculated in both the original
185 and each of the simulated datasets. If the model is an adequate description of
186 the original dataset, the observed test statistic should fall within the distribution
187 of the corresponding statistic of the simulated datasets, whereas potential
188 discrepancies could indicate that the chosen model does not capture specific
189 properties of the original dataset. The used test statistics were: M_{SIG} is the
190 mean of squared independent contrasts and refers to the measure of the overall
191 evolutionary rate; C_{VAR} is the coefficient of variation for the absolute contrasts

and identifies whether the rate heterogeneity is being assumed properly by the evolutionary model; S_{VAR} and S_{ASR} are based on estimates of slopes from fitting the linear model of the absolute contrasts values with the expected variances, and with the inferred ancestral state at a given node, respectively. The former allows for testing if the evolutionary rates are related with the branch lengths, whereas the latter is used to test whether the rates are related with the trait values; S_{HGT} measures the slope of a linear model of the absolute contrast values against the height of the node to evaluate its variation with respect to time; finally, the D_{CDF} which uses the D-statistic to compare if the distribution of the independent contrasts follows the normal distribution, as expected for the contrasts under Brownian motion (Pennell et al. 2015). It is important to note that the tested statistics were not used during the simulation themselves, such that their comparison would reveal specific ways in which the empirical dataset varies from expectations based on simple models of evolution.

We investigated variation in rates of climatic niche evolution using methods that assess changes both over time and among lineages. Temporal variation in climatic niche evolution was studied using the *phenogram* function in PHYTOOLS 0.4-45 (Revell 2012), where the phylogeny is plotted such that the position of each node on the Y-axis corresponds to the maximum likelihood estimate of the corresponding ancestral state. In addition, we investigated variation in climatic niche evolution among lineages using Accommodating Uncertainty in Trait Evolution Using R (AUTEUR; Eastman et al. 2011), as implemented in the AUTEUR package 0.12.0118 (Eastman et al. 2011). This method performs a Bayesian analysis using the reversible jump Markov chain Monte Carlo (rjMCMC), which allows the determination of the number, location,

and direction of the shifts on a given phylogeny by comparing models with different numbers of evolutionary rates (Eastman et al. 2011). Each AUTEUR analysis was run for 10,000,000 generations, with chain sampling every 1000 generations, and repeated twice to ensure convergence. We compared the obtained results with a second approach called Models of Trait Macroevolution on Trees (MOTMOT; Thomas and Freckleton 2011). Although these two methods share the property of not requiring the specification of the number and position of potential shifts beforehand, they differ considerably in their statistical approaches, such that a comparison of their results should provide a more robust inference regarding variation in rates of climatic niche evolution among lineages. However, given their considerable overlap in their objectives, we only present the MOTMOT analysis as supplementary material (Figure S1).

Results

The loadings from the PCA of primate climatic niches are shown in Table 1. The PCA was efficient in summarizing the main trends in the dataset, given that the first three PCs selected according to the broken-stick criterion accounted for 84% of the variance in the dataset (Table 1). The first PC reflected variation in temperature, particularly during the coldest/driest months, whereas the second PC indicated a negative relationship between temperature and precipitation, particularly during the warmest months. Finally, the third PC reflected mostly variation in precipitation, especially during the warmest/wettest months (Table 1). Interestingly, the distributions of each of the three primate clades on the PCA ordination plot were highly congruent, with most species being found in conditions of warm temperatures and mild winters (Figure 1).

242 Catarrhini showed considerably broader climatic niches in relation to other
243 clades, particularly on the first PC, which reflects their distribution into regions
244 with colder temperatures and more pronounced seasonality (Figure 1).
245
246 **Table 1.** Loadings of a Principal Components Analysis of primate climatic
247 niches. The first three principal components were selected based on the
248 broken-stick criterion.

Variables	PC1	PC2	PC3
Altitude	-0.24	0.22	-0.12
Annual Mean Temperature	0.28	-0.23	0.02
Mean Diurnal	-0.14	-0.25	-0.16
Isothermality	0.26	0.11	-0.25
Temperature Seasonality	-0.27	-0.03	0.18
Max Temperature of Warmest Month	0.15	-0.38	0.04
Min Temperature of Coldest Month	0.32	-0.06	-0.06
Temperature Annual Range	-0.27	-0.17	0.09
Mean Temperature of Wettest Quarter	0.20	-0.28	0.16
Mean Temperature of Driest Quarter	0.30	-0.14	-0.08
Mean Temperature of Warmest Quarter	0.20	-0.32	0.12
Mean Temperature of Coldest Quarter	0.30	-0.14	-0.07
Annual Precipitation	0.22	0.27	0.23
Precipitation of Wettest Month	0.10	0.05	0.52
Precipitation of Driest Month	0.20	0.29	-0.05
Precipitation Seasonality	-0.17	-0.30	0.23
Precipitation of Wettest Quarter	0.12	0.10	0.52
Precipitation of Driest Quarter	0.21	0.30	-0.06
Precipitation of Warmest Quarter	-0.04	0.20	0.39
Precipitation of Coldest Quarter	0.23	0.19	-0.03
Standard deviation	3.07	2.14	1.65
Proportion of Variance	0.47	0.23	0.14
Cumulative Proportion	0.47	0.70	0.84

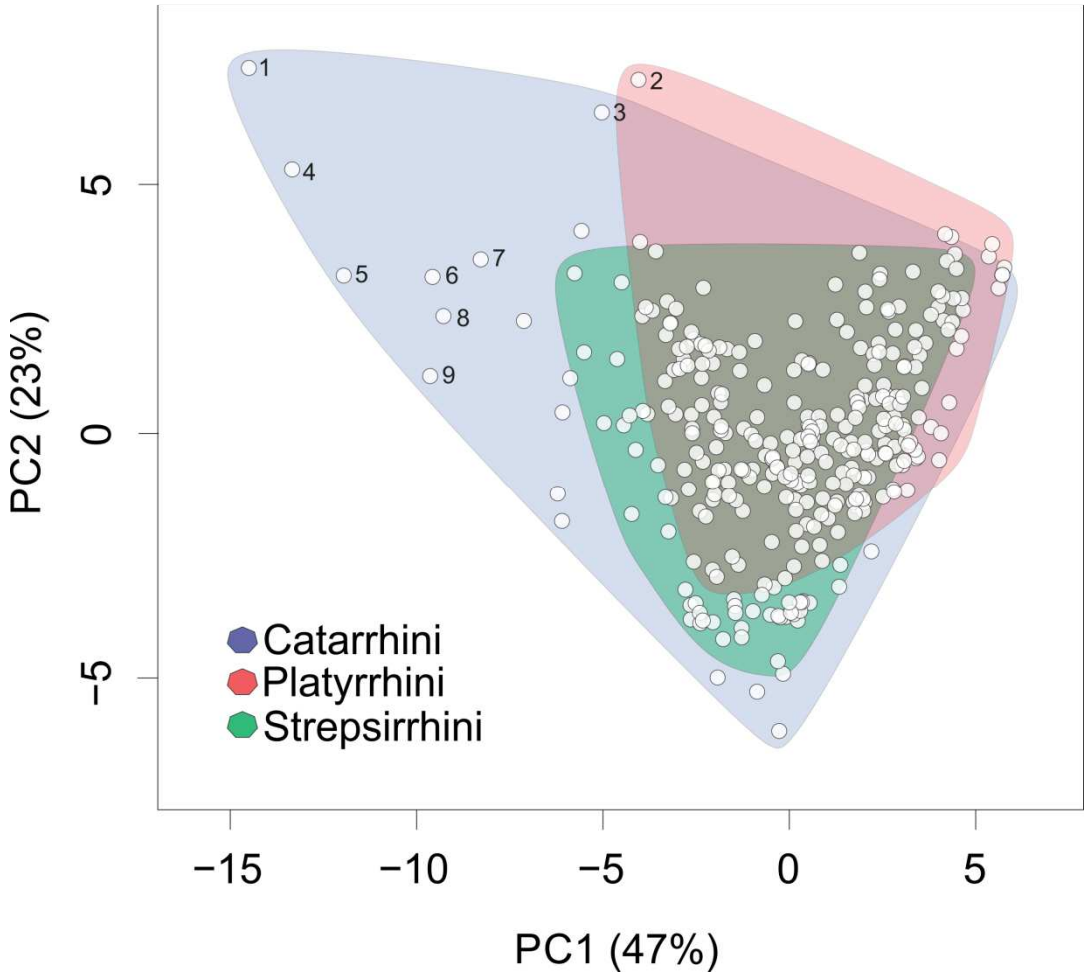

Figure 1. Scores along the first two PC axes representing the climatic niche space of primate species. Each data point represents the mean score for a given species. The numbered points represent species that occupy extreme regions the climatic niche space: (1) *Rhinopithecus bieti*, (2) *Aotus lemurinus*, (3) *Gorilla beringei*, (4) *Macaca munzala*, (5) *R. roxellana*, (6) *R. brelichi*, (7) *M. fuscata*, (8) *M. thibetana*, and (9) *M. sylvanus*. Low score values in PC1 indicate lower temperatures, particularly in coldest months, whereas high score values in PC2 indicate colder climatic conditions, with low mean temperatures during warmest months.

A comparison of model fit based on AIC indicated that OU was the best-fit model of trait evolution for all three PCs (Table 2). However, analyses of absolute fit based on posterior predictive simulation indicated an overall poor adequacy of the OU model to the data, particularly because they do not account

for variation in rates of evolution (Figure2). Significant departures from the simulated statistics were common, particularly with respect to C_{VAR}, S_{VAR}, and S_{ASR} (Figure 2). Moreover, the direction of bias also varied among clades, with alternating patterns of statistics being higher or lower than expected (Figure 2). In general, these results are consistent with substantial variation in rates in the analyzed datasets (heterotachy), suggesting that the interpretation of simple models that assume constant rates across the entire phylogeny might be misleading.

Table 2. Fit of the macroevolutionary models with respect to primate climatic niche axes. Bold values indicate the lowest AIC estimates for each PC among the tested models.

		Brownian Motion (BM)	Ornstein-Uhlenbeck (OU)	Early Burst (EB)
PC1	logL	-849.14	-794.35	-849.14
	AIC	1702.31	**1594.76**	1704.35
	α		20.61	
	a			0
PC2	logL	-779.6	-702.25	-779.6
	AIC	1563.25	**1410.56**	1565.28
	α		31.73	
	a			0
PC3	logL	-698.37	-607.28	-698.37
	AIC	1400.77	**1220.62**	1402.81
	α		36.94	
	a			0

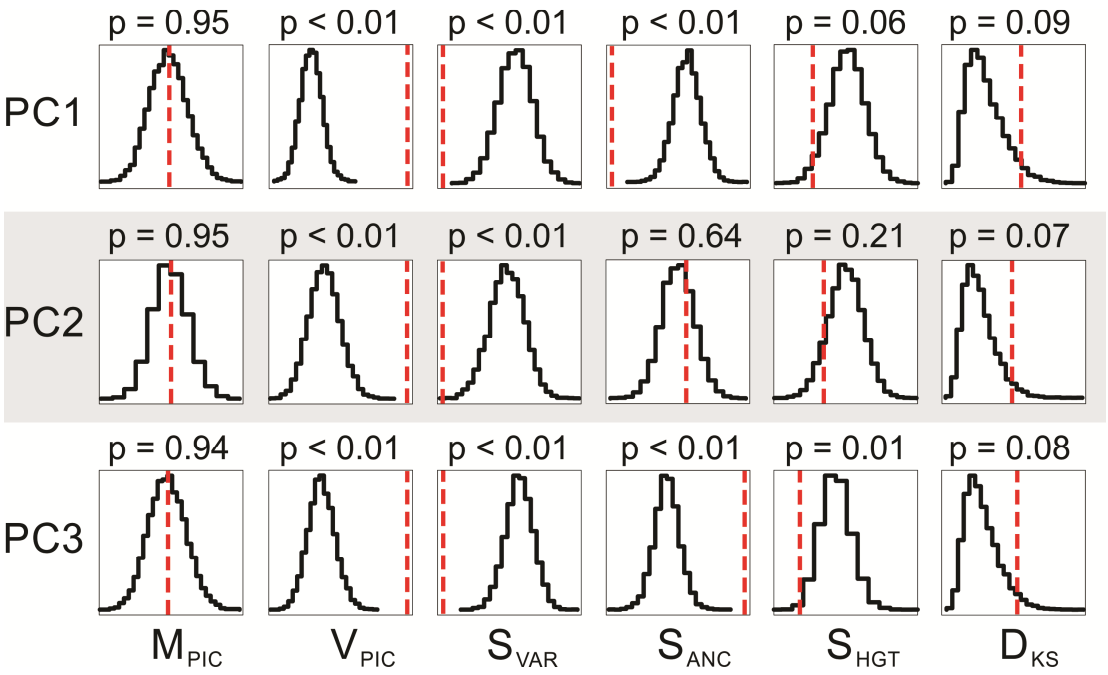

Figure 2. Distribution of test statistics based on posterior predictive simulation of three PC scores of primate climatic niches (black lines), observed statistics (dashed red lines) and their respective p-values. See text for more details about each statistic.

When variation in rates through time was assessed based on the reconstruction of ancestral states, a consistent pattern was uncovered indicating an apparent late increase in the rate of evolution of climatic niches, particularly during the past 10 My, most notably for catarrhines (Figure 3) Interestingly, the lineages occupying distinct regions of climatic space, as indicated in Figure 1, seem to have occupied these regions fairly recently (Figure 3). Likewise, AUTEUR analyses detected frequent shifts in rates of climatic niche evolution among lineages (Figures4 and S2. See also Figure S1 for the corresponding analysis using MOTMOT). Regardless of the niche axis, most lineages shared a similar background rate of climatic niche evolution, with many shifts distributed throughout the phylogeny involving few species in relatively recent nodes, such as *Piliocolobus gordonorum, P. kirkii, P.*

296 *rufomitratus, P. tephrosceles, and P. foai* on PC1 or the *Rungwecebus kipunji*
297 on PC2, and *Trachypithecus geei* and *T. johnii* on PC3 (Figures 4 and S2).
298 Interestingly, lineages that show rate shifts in PC1 are different from those
299 showing rate shifts on PC2. Finally, the vast majority of the identified shifts
300 involved rate increases (Figure 4 and S2), suggesting that decreases in rates of
301 climatic niche evolution of primates are rare, with only two cases of rate
302 decrease across all analyses on PC1 and PC2. The first included the entire
303 infraorder Lemuriformes (Strepsirrhini) in PC1, but the support for this specific
304 shift rate was low based on the AUTEUR method (Figure 4). The other rate
305 decrease was observed in some of the species of *Macaca*, in the Catarrhini
306 clade, but in this case with strong support. Coincidently, both of these instances
307 occurred with species that live in islands (Madagascar in Africa and the
308 Sulawesi in Indonesia, respectively). In general, the greatest number of rate
309 shifts was detected in Catarrhini, with strong support for rate shifts in all the
310 three PCs. These shifts were detected in lineages from southern and
311 southeastern from Asia, and in species from Africa. Only one case of shift rate
312 with strong support occurred in South America, comprising species of
313 *Leontopithecus* (Figure S3).
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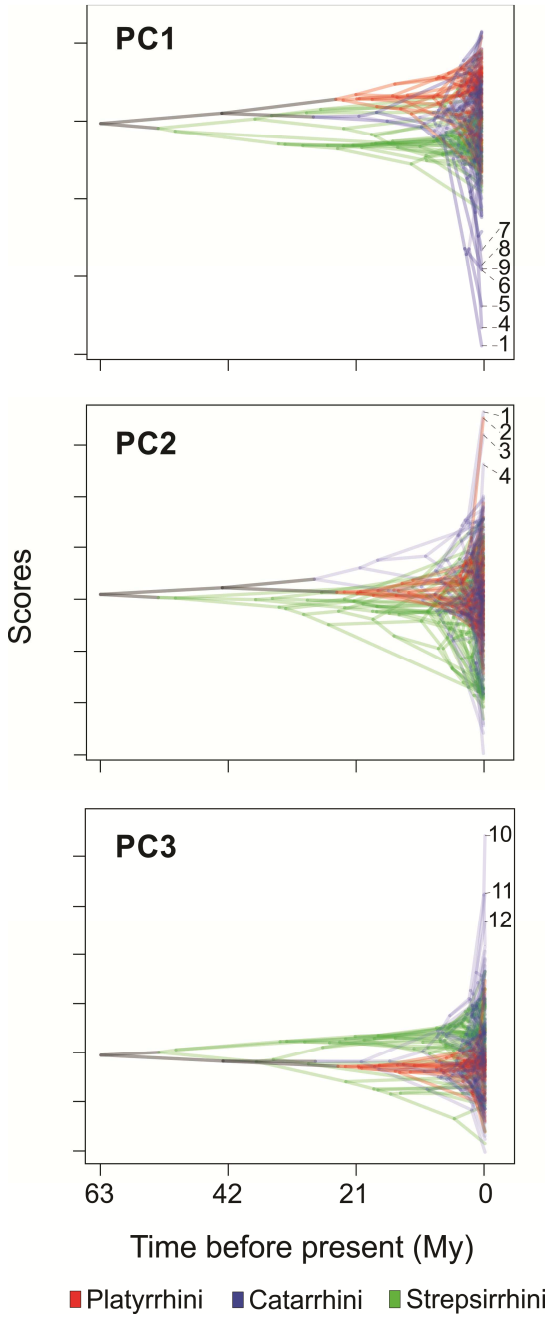
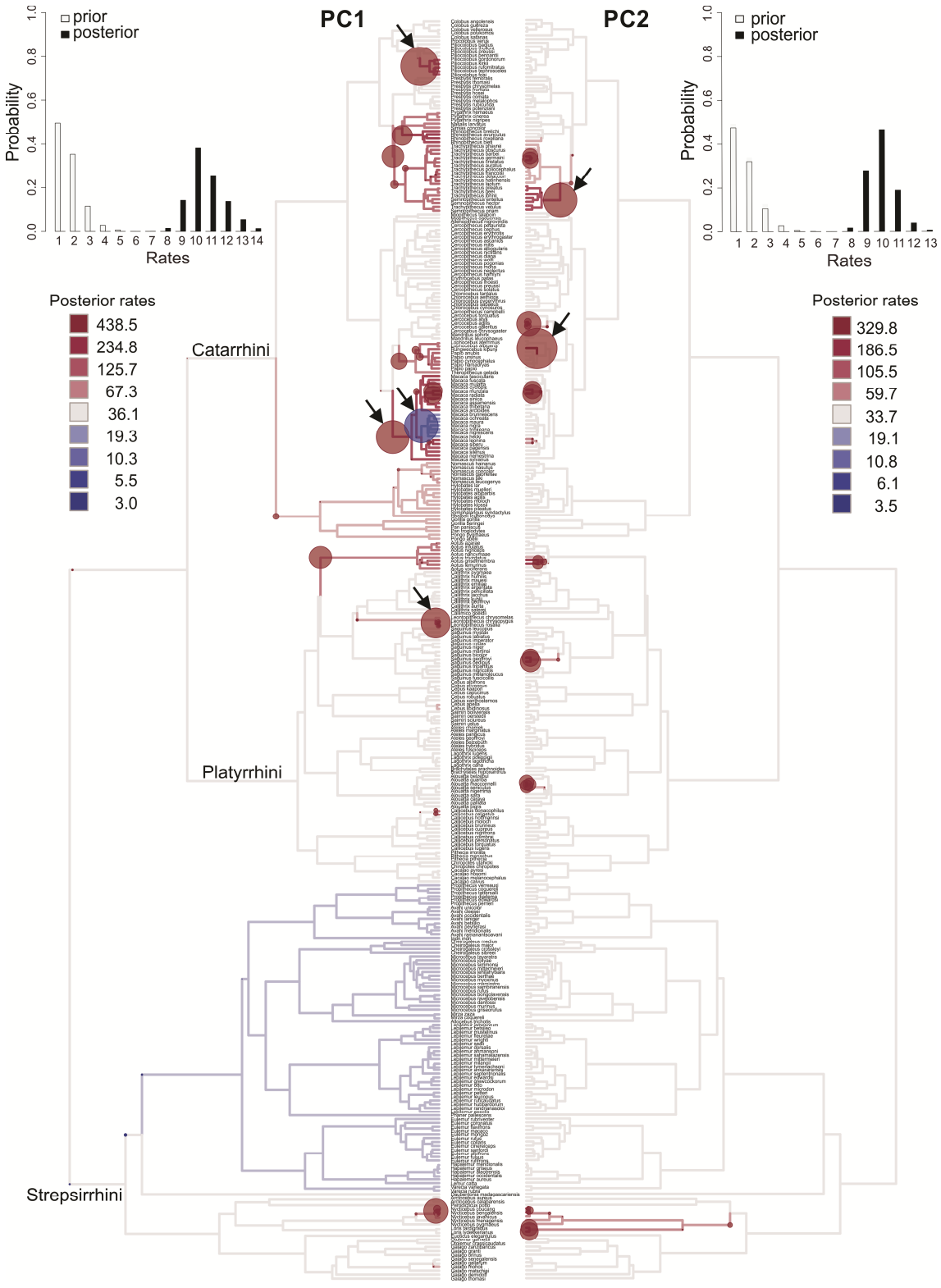


320

321 **Figure 3**. Reconstruction of ancestral states along primate climatic niche axes.
322 The position along the x-axis corresponds to the node age in millions of years
323 and the y-axis positions corresponds to the reconstructed character value
324 based on PC scores. Each of the three clades is distinguished by colors
325 indicated in the legend. Catarrhini, in blue, shows the broadest variation in
326 climatic niche occupation in all three PCA axes. The number in divergent
327 branches corresponds to the species indicated in Figure 1, following the same
328 order from that legend, with three additional species in PC3: (10)
329 *Trachypithecus geei*, (11) *Macaca silenus* and (12) *T. laotum*.



330

331 **Figure 4.** Posterior rate estimates of primate climatic niche evolution based on
332 the AUTEUR method, indicating how the shift rates varied across the
333 phylogeny. Background rates are shaded in grey, whereas background
334 deviating rates are shaded in darker colors according to the posterior rates in
335 the legend. Circles correspond to level of the support for each shift. We added

arrows to indicate rate shifts with the strongest support. Interestingly, all species indicated in Figures 1 and 3 are shown here as experiencing shifts in rates of climatic niche evolution. See text for details.

Discussion

The results of the present study provide a comprehensive view of how climatic niches evolved over the course of the history of Primates. First, the occupation of climatic space was not homogeneous among primate lineages, with most species being concentrated under relatively mesic conditions (i.e. warm temperatures and mild winters - Figure 1 and Table 1). In addition, primate climatic niche evolution was characterized by considerable heterotachy, given the low adequacy of simple models of evolution (Figure 2) and the detection of multiple rate shifts (Figure 4). Finally, even though these shifts occurred independently in several lineages and niche axes, they tended to be more frequent near the present (Figure 3). It is noteworthy that ancestral character reconstructions clearly show that all clades showed more pronounced evolution of climatic niches near the present, particularly in past 10 My (Figure 3). Despite the inherent uncertainties surrounding the reconstruction of ancestral characters (Schluter et al. 1997),the consistent pattern in different clades, which live across geographically distinct locations, suggest that this pattern is robust, particularly in the case of Catarrhini. Results based on paleoclimatic and paleovegetational data suggest severe climatic changes in the globe over the past 65 My, including glacial and interglacial cycles (e.g. Zachos et al. 2001). In particular, the period from approximately 23 to 5 My, comprising the Miocene period, included several anomalous cooling phases characterized by shorter periods of smaller glaciations (Zachos et al. 2001).

These observations match our results, suggesting that the diversification of the primate climatic niches could be a consequence of Earth's cooling in this period. Interestingly, lineage diversification itself seems to have been accelerated over the past ≈7 My (see Figure 8 in Springer et al. 2012), suggesting a possible causal relationship between both rates, as suggested for salamanders (Kozak and Wiens 2010a). Changes in vegetation during the Miocene are also thought to be related with the global cooling (Briggs 1995; Dutton and Barron 1997). Together with paleoclimatic variation, the vegetational changes seem to correlate with the diversification of primates climatic niches in the present study, particularly given the importance of forest architecture to primate community structure and richness (Gouveia et al. 2014). The biogeographic history from Platyrrhini, for instance, suggests that this neotropical clade evolved in South America for more than 26 My and experienced changes in fauna, continent structure, climate, and flora, with the Amazonian rain forest starting to reach its current configuration at about 15 My (Rosenberger et al. 2009). Similarly, the catarrhine family Cercopithecidae arose in early Miocene (Briggs 1995) and their diversification also seems to be related with changes in their climatic niches, particularly in the case of *Macaca* and *Trachypithecus* (see Figure 3). Moreover, the relatively distinctive evolutionary patterns found in SE Asian primates are also reflected in their correlates of species richness, which seem to be more associated with precipitation than other primate lineages (Gouveia et al. 2014).

The extensive variation in rates of climatic niche evolution among the primate lineages (see Figure 4) generally occurred near the present, in agreement with the results discussed above. Interestingly, there was

quantitative variation in the magnitude of the shifts among primate clades. Catarrhini shows more frequent changes in evolutionary rates (Figures 4) and the climatic niche divergence in this clade was markedly higher (Figure 3). On the other hand, shifts in Platyrrhini and Strepsirrhini were less severe despite their substantial lineage diversification, suggesting that, for these clades, species diversification and the climatic niche evolution were at least partially uncoupled. It is important to acknowledge that error in PC scores could potentially contribute to the observed pattern of recent shifts in rates of climatic niche evolution, given that they would falsely imply that the niches of the involved species would have experienced a severe change in their recent evolutionary past in comparison with its closely related species. However, we believe that this effect is not capable of producing the results obtained in our study given that the vast majority of the detected shifts were not reconstructed on terminal branches (as one would expect in the case of measurement error on a single species). In addition, the consistency in terms of timing and geographical distribution of the involved species is strongly suggestive of a real biological mechanism underlying those shifts.

A suggestive pattern presented with our analysis is the observation that several of the lineages with significant rate shifts have their geographic distribution related to mountain ranges (Figure S3). Examples include the catarrhine *Macaca sylvanus*, which lives in the Atlas Mountains in northwestern Africa, the *Rungwecebus kipunji*, which has a very restricted distribution in Udzungwa and Livingstone Mountains in southern Tanzania, and the primate species from southern and southeastern Asia, which may be influenced by the mountain range of the Himalayas (Figure S3). One could hypothesize that these

changes in evolutionary rates could be linked to different climatic conditions and gradients in these regions. An intriguing finding related to these mountainous environments and with the changes in evolutionary rates is that the species presented in Figure S3 inhabit regions strongly influenced by the monsoon systems, except for the South America species. The two strongest monsoons on Earth occur in the Asian-Australian system and in western Africa (Trenberth et al. 2000) and are strongly related with the Himalayas mountain ranges (Webster et al. 1998). India, for instance, has the monsoons as the major weather phenomenon (Overpeck et al. 1996), and all the primates include in our analyses that occur in this region exhibit rate shift in climatic niche evolution.

Although there is increasing evidence for a crucial role of climatic conditions in determining mammal species distributions and their fluctuations over time (e.g. Smith 2013), it is important to recognize that other factors, such as dispersal capacity (Seifer et al. 2015) and biotic interactions (Holt and Barfield 2009) might play an important role in determining geographical range limits. The extent to which these factors drive primate distributions is still poorly understood, yet their recognition does not contradict the results of our study. In particular, our analyses are based on the climatic conditions actually experienced by different species throughout their entire range. Such conditions could either directly affect the physiological tolerance of a given species or indirectly impact the strength of its biotic interactions, and we are agnostic with respect to the relative importance of these potential direct and indirect effects. As a consequence, climatic and biotic drivers of geographical distributions do not represent mutually-exclusive mechanisms, yet understanding their interplay

over the course of the evolutionary history of a clade is a major challenge for future studies.

This study underscores the potential of recently developed phylogenetic comparative methods in uncovering complex dynamics in the evolution of climatic niches. Many studies, particularly in the context of environmental niche modeling, tend to assume that climatic niches are static, yet little is known about how niches evolve when that assumption is not met (Pearman et al. 2008). In this study we demonstrate extensive heterotachy in evolutionary rates in primate climatic niches, revealing the location, number and direction of changes in rates in lineages and the differences among clades. In addition, many models commonly used in studies of character evolution showed poor absolute fit to our dataset, deviating in several ways from the general statistics investigated through posterior predictive simulation. This suggests that more realistic evolutionary models must be considered in order to better describe the evolutionary pattern of climatic niche evolution in primates. We raised several important points that should be investigated carefully in future studies, such the suggested relationship between the rate shifts with the mountain ranges and monsoons systems, which should also be explored for different taxa. Finally, we showed how the rate of climatic niche evolution can be affected by global-scale changes in world climate, particularly over the past 10 My, providing important expectations for future studies on other model systems.

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Supporting Information

Table S1. Raw data from the 334 primate species with their respective mean values for the 20 variables used in PCA analysis.

spp	alt	bio_1	bio_2	bio_3	bio_4	bio_5	bio_6	bio_7	bio_8	bio_9	bio_10	bio_11	bio_12	bio_13	bio_14	bio_15	bio_16	bio_17	bio_18	bio_19
Allocebus_trichotis	671.17	211.34	100.44	64.78	2240.37	286.86	133.32	153.54	235.92	191.32	236.21	180.30	1892.81	327.36	48.37	66.22	916.28	186.10	913.52	237.82
Arctocebus_aureus	441.01	243.62	97.38	77.40	782.31	308.07	182.79	125.27	242.78	236.55	252.17	232.53	1761.31	286.49	26.77	54.12	703.18	123.48	516.02	258.01
Arctocebus_calabarensis	343.44	254.06	90.90	73.58	985.83	322.30	199.03	123.27	241.62	258.82	266.70	240.70	2267.63	374.17	17.74	67.52	1022.76	83.50	326.59	1008.80
Avahi_betsilio	1274.26	177.46	111.04	63.32	2586.96	260.22	86.38	173.84	204.91	150.25	205.22	141.23	1686.09	307.19	41.67	73.91	864.42	132.96	858.57	150.78
Avahi_cleesei	373.01	246.50	125.32	65.26	1838.78	329.65	138.97	190.68	260.45	218.74	262.98	217.71	1316.02	349.39	2.02	109.37	876.78	11.91	455.97	11.91
Avahi_laniger	710.52	209.40	101.88	64.70	2267.85	285.48	129.43	156.06	234.15	188.30	234.41	177.99	1883.62	332.25	46.44	68.67	926.75	178.60	918.93	229.10
Avahi_meridionalis	425.22	213.91	108.36	62.61	2446.12	292.91	121.22	171.69	241.39	190.41	241.71	179.50	1543.35	246.77	52.40	54.40	690.13	194.42	667.25	236.07
Avahi_occidentalis	122.77	265.22	127.88	67.99	1451.93	350.70	163.74	186.96	273.55	243.78	279.34	242.86	1518.35	450.83	1.08	121.06	1076.07	5.26	565.25	5.26
Avahi_peyrierasi	956.97	194.37	108.18	63.65	2531.00	275.15	106.49	168.65	221.54	170.33	221.84	159.15	1794.67	332.35	41.67	73.49	927.26	153.64	913.41	188.80
Avahi_ramanantsoavani	31.29	232.71	87.86	56.57	2353.71	304.86	151.14	153.71	260.71	213.71	260.71	200.71	2374.86	341.14	80.86	45.29	1002.71	311.57	1002.71	409.14
Avahi_unicolor	399.88	242.05	105.21	71.47	1326.14	307.10	160.94	146.16	252.61	222.29	253.90	222.26	1790.10	441.10	12.16	101.37	1120.03	43.17	820.51	43.63
Cheirogaleus_crossleyi	593.00	217.33	104.00	66.33	2135.00	291.67	136.33	155.33	240.33	194.33	240.33	188.33	1478.67	285.33	34.00	74.67	763.00	132.33	763.00	163.33
Cheirogaleus_major	698.70	210.43	105.18	65.09	2217.62	286.72	126.29	160.42	233.93	188.27	234.36	179.33	1795.28	334.37	40.75	73.84	922.18	154.15	888.10	192.91
Cheirogaleus_medius	204.92	249.23	128.76	65.47	2212.68	334.73	138.94	195.79	270.21	218.92	271.54	216.69	967.95	266.57	4.17	108.69	659.16	17.00	491.81	19.84
Cheirogaleus_sibreei	1462.00	165.50	113.00	63.50	2564.50	247.50	71.50	176.00	192.00	129.00	192.50	129.00	1433.50	287.00	24.50	85.50	789.00	78.50	774.00	78.50
Daubentonia_madagascariensis	612.47	217.15	105.96	65.07	2151.58	292.81	131.26	161.55	239.39	194.74	240.00	186.66	1719.91	339.20	35.74	80.22	914.54	134.90	846.21	170.55
Eulemur_cinereiceps	738.88	203.05	103.08	61.29	2489.61	279.52	112.82	166.70	229.19	179.78	229.83	167.23	1595.30	302.62	40.09	77.95	849.84	141.30	824.34	166.77
Eulemur_coronatus	245.45	249.54	94.18	71.17	1273.57	309.38	177.94	131.44	260.71	234.49	261.17	230.84	1438.05	334.51	18.75	95.61	877.69	73.45	787.35	78.55
Eulemur_albifrons	577.79	217.03	97.07	65.08	2120.61	290.36	142.94	147.41	240.10	200.25	240.59	187.23	2102.75	337.98	58.46	58.30	954.61	219.99	950.06	295.79
Eulemur_collaris	731.63	201.42	111.23	62.91	2503.85	281.91	106.53	175.37	228.76	172.85	229.01	165.75	1491.37	274.47	38.14	70.37	757.66	140.92	749.47	163.41
Eulemur_fulvus	618.88	221.89	112.35	65.86	2056.32	301.36	132.08	169.28	241.81	198.35	243.34	192.78	1660.77	369.66	24.14	91.92	969.57	94.54	810.07	115.42
Eulemur_rufus	130.94	258.80	115.79	66.46	1688.99	332.31	158.96	173.36	271.73	233.31	273.90	232.78	1259.04	373.64	1.79	120.43	892.55	9.57	577.69	9.63
Eulemur_sanfordi	287.00	247.68	93.60	71.16	1265.50	307.49	176.81	130.67	258.82	233.19	259.24	229.12	1415.39	342.79	16.11	99.78	886.07	63.64	810.04	69.32
Eulemur_flavifrons	310.90	248.31	108.63	72.26	1228.76	315.50	166.14	149.36	257.17	229.68	258.83	229.65	1721.78	437.55	8.07	105.29	1101.29	27.93	780.22	28.25

Eulemur_macaco	421.54	240.24	105.85	70.40	1395.19	306.87	157.66	149.22	251.69	219.81	252.73	219.55	1806.46	430.63	15.43	98.88	1115.64	54.19	856.67	56.29
Eulemur_mongoz	90.82	265.87	117.28	68.82	1373.30	341.56	171.92	169.64	273.66	245.68	278.68	244.58	1477.49	447.14	1.13	122.33	1052.45	5.87	509.63	5.89
Eulemur_rubriventer	919.55	200.28	109.82	66.08	2260.08	279.50	114.55	164.95	224.11	176.73	224.36	168.48	1661.59	324.50	34.49	78.85	891.94	128.40	873.10	149.45
Eulemur_rufifrons	398.86	234.74	131.01	63.25	2529.87	323.88	118.58	205.30	260.05	200.92	260.69	197.92	937.97	238.67	9.44	108.98	605.30	32.97	552.50	37.01
Euoticus_elegantulus	446.12	243.63	96.99	76.31	821.86	308.40	181.73	126.66	243.29	235.87	252.60	231.92	1727.53	280.06	24.53	55.50	693.11	112.90	509.28	251.68
Galago_gallarum	421.23	264.97	129.56	75.12	1196.26	357.81	186.76	171.05	271.96	257.78	279.85	248.75	437.92	116.94	2.93	99.71	222.42	16.79	132.18	39.61
Galago_matschiei	1514.81	197.65	112.54	85.67	365.75	264.42	133.73	130.69	196.59	196.08	201.76	192.91	1416.61	180.34	42.78	36.96	486.81	174.90	333.75	282.17
Galago_moholi	1038.54	215.17	136.17	61.09	2333.21	315.44	91.48	223.96	230.75	182.30	238.23	180.71	932.35	196.30	1.24	97.01	531.82	7.22	282.98	13.36
Galago_senegalensis	660.82	255.27	136.50	66.12	1761.01	358.65	149.83	208.83	250.85	242.97	278.57	233.25	880.77	201.99	4.45	102.59	504.61	20.91	147.65	204.86
Galago_demidoff	526.25	245.74	106.22	76.14	791.09	316.92	176.31	140.61	242.84	241.89	255.14	235.19	1674.11	263.95	27.66	56.22	685.67	118.76	394.16	357.24
Galago_granti	255.76	241.83	115.86	63.11	2211.39	326.32	142.82	183.50	261.57	220.71	264.39	209.20	990.95	210.50	9.35	90.25	576.16	37.09	437.57	49.97
Galago_orinus	1533.98	187.98	106.72	65.55	1544.35	268.26	106.77	161.49	197.10	168.69	204.32	165.14	1043.64	216.69	6.99	89.60	565.59	28.99	300.50	32.28
Galago_thomasi	588.73	241.94	107.10	75.69	804.36	312.53	169.91	142.62	240.86	235.97	250.91	230.84	1633.81	259.19	25.89	58.24	670.67	111.24	405.74	301.82
Galago_zanzibaricus	487.12	241.70	97.01	65.80	1620.03	310.82	164.78	146.04	251.15	221.76	259.72	218.79	1234.94	268.39	20.74	72.39	610.65	76.60	363.24	86.31
Hapalemur_aureus	1036.95	187.08	102.83	60.93	2517.45	265.35	98.08	167.28	213.13	164.22	213.48	150.76	1523.76	315.24	36.20	81.24	836.59	119.95	828.33	135.81
Hapalemur_griseus	730.66	210.17	107.21	63.90	2292.05	287.35	120.85	166.50	233.50	186.43	234.32	177.66	1729.39	354.93	34.71	84.30	947.43	130.54	858.30	163.86
Hapalemur_alaotrensis	755.90	210.40	127.30	67.30	2360.40	298.20	110.70	187.50	235.80	180.10	235.80	177.30	1144.40	279.60	4.00	107.10	740.50	20.80	740.50	25.90
Hapalemur_meridionalis	694.99	202.35	110.86	62.95	2493.64	282.48	107.77	174.71	229.84	174.84	230.06	166.91	1512.32	269.45	41.16	66.78	747.49	153.55	737.55	178.55
Hapalemur_occidentalis	604.45	217.80	100.75	66.14	2032.38	291.21	140.37	150.85	239.34	198.73	239.83	189.43	1890.53	345.58	42.52	71.88	951.30	161.84	898.39	207.89
Indri_indri	796.64	204.33	103.90	64.91	2352.36	282.14	123.35	158.79	230.11	181.58	230.24	171.96	1791.34	327.04	41.44	72.18	916.04	161.05	912.35	198.36
Lemur_catta	321.00	238.66	140.25	64.19	2710.16	334.29	117.73	216.57	266.91	203.59	267.28	199.54	681.39	170.56	5.62	100.28	443.90	21.16	414.02	26.07
Lepilemur_aeeclis	89.01	266.62	114.93	69.38	1326.00	340.57	175.83	164.74	273.30	248.76	279.44	245.89	1494.75	451.56	1.16	121.33	1053.60	6.95	388.23	7.09
Lepilemur_ahmansoni	140.53	259.67	114.61	68.53	1443.68	329.87	163.72	166.14	268.78	237.66	272.20	237.24	1370.14	409.96	1.61	121.76	974.71	9.27	546.53	9.29
Lepilemur_ankaranensis	412.34	239.92	95.73	71.95	1284.92	300.33	168.05	132.28	251.34	225.56	251.62	221.15	1429.00	342.19	15.90	99.24	890.18	62.96	818.95	69.10
Lepilemur_betsileo	983.47	190.46	107.61	62.97	2537.09	271.26	101.70	169.56	217.35	166.36	218.00	155.11	1931.94	349.17	46.03	70.15	965.66	165.26	929.08	214.45
Lepilemur_dorsalis	722.01	223.17	114.87	70.48	1557.73	297.27	135.60	161.67	236.79	200.73	237.45	200.39	1687.73	392.58	14.52	99.33	1042.30	50.49	868.04	53.57
Lepilemur_edwardsi	72.59	266.85	121.31	67.20	1447.50	346.37	166.80	179.58	275.12	247.33	280.34	244.52	1499.33	450.70	1.16	121.92	1065.01	5.80	546.68	5.81
Lepilemur_fleuretae	503.74	213.80	119.32	63.56	2600.15	298.32	112.41	185.91	242.47	185.73	242.72	176.97	1341.83	244.55	34.86	69.09	675.74	128.80	666.90	152.86
Lepilemur_grewcockorum	67.22	265.09	119.15	67.86	1435.28	343.63	168.90	174.72	273.93	242.64	277.67	242.62	1552.79	454.61	1.79	118.97	1085.61	7.25	454.83	7.25
Lepilemur_hubbardorum	300.83	240.84	141.44	64.42	2620.56	336.66	118.88	217.78	268.03	204.22	268.56	202.86	645.75	170.51	2.77	108.60	440.66	12.21	404.43	12.43
Lepilemur_jamesorum	703.61	204.88	104.08	61.51	2499.06	281.52	113.72	167.80	231.08	181.15	231.88	168.97	1618.24	311.12	39.86	78.75	872.47	139.91	837.39	164.10

Lepilemur_leucopus	206.41	237.46	138.05	64.18	2924.72	333.22	120.28	212.94	269.74	205.28	269.75	196.37	547.35	109.35	9.97	77.73	306.82	34.98	306.03	52.43
Lepilemur_microdon	867.85	194.36	104.23	61.13	2522.24	273.35	104.24	169.11	220.59	172.52	221.20	158.39	1772.33	354.34	42.06	77.35	949.75	147.42	908.57	181.01
Lepilemur_milanoii	155.03	252.40	93.15	71.30	1335.08	311.13	181.47	129.66	264.97	236.47	265.05	232.88	1425.84	285.67	27.91	79.67	784.35	108.95	730.81	113.32
Lepilemur_mittermeieri	119.82	258.51	89.28	70.68	1171.14	312.70	187.33	125.37	267.37	240.74	268.98	240.74	1936.88	476.63	16.46	97.44	1190.96	59.19	798.84	59.19
Lepilemur_mustelinus	855.05	201.77	107.93	64.37	2442.64	281.64	115.45	166.19	228.34	175.97	228.46	168.09	1769.24	329.06	38.28	75.82	919.58	151.15	913.13	188.90
Lepilemur_otto	85.94	264.62	131.81	64.73	1767.87	354.38	152.17	202.21	276.02	238.12	281.25	237.58	1523.41	462.03	1.00	124.06	1106.94	5.01	779.58	5.01
Lepilemur_petteri	173.69	242.10	133.83	62.97	2856.62	336.35	125.86	210.49	273.60	207.94	273.64	201.73	497.01	114.75	5.49	92.03	309.86	22.94	306.48	27.70
Lepilemur_randrianasoloi	145.92	256.32	116.91	65.55	1803.76	331.86	154.61	177.25	271.17	229.20	272.52	228.60	1220.85	352.31	2.09	117.85	853.33	10.62	600.63	10.62
Lepilemur_ruficaudatus	140.22	253.95	135.62	63.14	2455.20	342.63	129.49	213.14	277.25	217.83	278.15	217.83	851.05	254.98	1.15	122.56	615.01	5.32	526.06	5.32
Lepilemur_sahamalazensis	138.30	259.02	105.57	72.52	1101.23	323.85	179.26	144.59	266.01	241.96	268.13	241.96	1737.02	451.58	6.48	106.74	1122.13	22.36	737.94	22.37
Lepilemur_seali	626.39	214.78	100.00	65.48	2124.90	289.35	138.46	150.89	237.79	196.06	238.21	185.18	1948.45	330.96	50.77	64.43	921.62	191.39	917.96	252.12
Lepilemur_septentrionalis	89.76	260.00	86.06	69.94	1222.53	317.00	194.71	122.29	271.59	247.53	271.59	241.94	1270.59	312.53	17.41	97.47	788.65	69.71	788.65	75.35
Lepilemur_tymerlachsoni	132.00	258.00	81.00	68.00	1288.00	311.00	193.00	118.00	269.00	239.00	270.00	239.00	2068.00	463.00	27.00	90.00	1225.00	95.00	1177.00	95.00
Lepilemur_wrighti	996.76	198.24	123.44	64.15	2598.26	286.25	95.20	191.05	225.70	164.20	225.70	160.37	1094.48	236.11	17.72	89.51	641.13	57.53	641.13	59.02
Loris_lydekkerianus	414.79	261.56	93.40	59.33	1820.37	343.94	185.15	158.79	254.23	255.84	285.39	237.90	1509.83	399.75	8.47	85.94	906.24	44.09	209.80	554.39
Loris_tardigradus	439.71	247.15	79.85	70.36	678.22	306.29	193.22	113.07	244.97	244.82	255.70	237.85	2878.87	395.28	104.10	38.32	1011.82	395.14	792.33	646.68
Microcebus_berthae	56.83	259.07	130.33	63.43	2230.87	341.11	137.15	203.96	278.83	225.72	280.00	225.72	930.48	295.09	0.98	125.39	675.02	3.74	560.09	3.74
Microcebus_bongolavensis	96.54	264.03	132.25	64.72	1776.27	354.25	151.32	202.94	275.53	237.21	280.77	236.85	1524.37	462.40	1.00	124.14	1108.16	4.91	789.34	4.91
Microcebus_danfossi	77.90	264.53	119.49	67.79	1436.72	343.22	167.89	175.33	273.39	242.04	277.09	242.04	1552.72	459.95	1.53	119.91	1089.52	6.54	431.51	6.54
Microcebus_griseorufus	162.57	240.03	134.94	63.56	2834.13	334.13	123.91	210.22	271.40	206.68	271.45	200.19	521.68	113.55	7.97	85.99	307.62	29.97	302.87	40.54
Microcebus_jollyae	77.79	229.84	94.68	59.57	2395.62	302.79	145.12	157.67	256.67	210.90	256.85	196.92	2300.20	376.50	72.99	55.01	1068.23	276.92	1020.07	361.90
Microcebus_lehilahytsara	974.92	194.08	108.58	63.17	2609.08	275.42	105.17	170.25	222.00	171.08	222.25	157.92	1890.00	336.17	53.08	68.00	953.00	187.67	944.67	230.00
Microcebus_mamiratra	70.00	262.36	75.21	66.93	1270.71	312.14	200.93	111.21	273.00	242.93	274.00	242.93	2063.86	454.86	29.14	88.43	1207.93	101.71	1163.07	101.71
Microcebus_mittermeieri	1214.22	189.11	119.56	70.56	2195.11	270.11	101.33	168.78	212.33	162.67	212.33	157.56	1680.33	322.89	38.56	74.22	885.44	145.89	885.44	149.89
Microcebus_murinus	191.14	250.93	129.41	65.27	2180.48	335.86	138.63	197.23	271.17	220.10	272.57	218.62	976.45	277.97	3.14	114.10	679.42	13.44	508.27	15.16
Microcebus_myoxinus	163.55	257.17	121.67	65.64	1807.53	334.95	150.32	184.63	271.10	229.63	273.36	229.17	1220.51	353.62	1.82	117.49	855.52	9.54	536.28	9.54
Microcebus_ravelobensis	135.69	263.99	128.95	68.03	1481.52	350.97	162.50	188.47	272.61	242.41	278.58	241.17	1524.71	448.12	1.37	120.21	1074.80	6.01	557.48	6.03
Microcebus_rufus	725.22	207.47	104.49	64.48	2283.60	284.27	123.58	160.69	232.09	185.26	232.42	175.57	1818.42	327.18	44.30	70.15	907.61	167.93	894.05	211.84
Microcebus_sambiranensis	396.34	242.33	105.03	71.50	1325.48	307.32	161.53	145.79	252.89	222.53	254.13	222.51	1782.78	440.16	12.01	101.59	1116.13	42.69	822.49	43.07
Microcebus_simmonsi	760.89	207.62	102.27	63.95	2382.05	285.33	126.91	158.42	234.39	181.53	234.39	174.89	1670.78	298.00	37.14	72.20	848.62	152.50	848.62	176.73
Microcebus_tavaratra	326.56	245.63	97.55	71.34	1265.95	307.46	171.54	135.92	256.26	230.19	256.96	226.96	1483.79	355.15	16.15	99.72	927.27	62.29	794.21	68.02

Mirza_coquereli	271.06	248.57	139.87	64.30	2397.34	341.11	125.34	215.78	271.02	213.56	272.03	212.79	881.00	247.87	2.23	114.37	611.83	9.89	488.64	10.01
Mirza_zaza	131.23	259.25	107.16	69.49	1344.49	325.69	172.44	153.25	268.38	238.74	270.89	238.60	1585.27	434.26	6.93	113.98	1068.38	25.59	652.09	26.06
Nycticebus_bengalensis	569.54	232.63	102.57	50.62	2870.80	320.42	117.13	203.29	253.53	195.99	262.78	190.38	1849.67	391.13	9.01	85.99	1039.59	44.66	684.08	68.43
Nycticebus_coucang	266.73	255.68	92.28	85.57	405.68	311.16	203.66	107.50	252.41	255.12	260.47	250.26	2557.69	335.86	110.68	34.36	909.10	376.81	616.86	723.79
Nycticebus_javanicus	368.13	249.33	93.87	81.70	414.91	305.81	191.59	114.22	247.94	245.78	253.21	243.39	2920.63	415.78	98.84	46.49	1133.82	332.96	734.42	664.11
Nycticebus_menagensis	246.73	255.78	78.73	88.73	290.97	301.97	213.55	88.42	254.11	255.93	258.52	251.58	3008.10	340.33	164.04	22.50	941.47	541.03	705.00	820.46
Nycticebus_pygmaeus	560.03	226.95	92.27	51.08	2868.69	308.22	126.88	181.35	249.66	191.56	257.95	185.80	1851.97	397.32	12.50	85.70	1037.18	60.50	715.77	90.25
Otolemur_crassicaudatus	934.48	219.89	126.80	64.11	1887.65	310.92	111.65	199.27	232.27	194.91	238.88	192.07	1031.21	208.23	3.92	90.79	559.28	18.39	319.89	27.85
Otolemur_garnettii	671.86	233.63	102.41	67.06	1463.26	307.55	156.34	151.22	241.96	217.05	249.34	212.41	961.65	207.01	7.67	87.49	521.16	31.92	304.72	47.16
Perodicticus_potto	536.21	244.28	104.49	77.68	724.72	312.86	178.32	134.53	241.93	240.84	252.63	234.34	1706.46	257.14	30.72	52.21	668.25	131.25	418.82	357.77
Phaner_pallescens	188.79	252.59	130.47	65.06	2155.03	337.38	137.82	199.56	272.13	221.09	273.54	220.41	983.32	286.65	1.86	117.43	695.92	8.84	511.28	8.91
Propithecus_coquereli	109.40	263.06	125.35	66.98	1577.48	347.08	160.92	186.15	273.16	239.52	277.61	238.78	1547.59	457.23	1.53	121.01	1095.66	6.56	627.35	6.60
Propithecus_diadema	759.57	205.59	103.29	64.15	2380.00	283.32	123.72	159.60	231.85	182.77	232.00	173.08	1834.50	331.56	43.06	71.74	927.79	167.88	923.18	209.68
Propithecus_edwardsi	1051.34	186.36	107.10	62.01	2549.42	267.14	95.87	171.28	212.91	162.25	213.43	150.11	1700.35	337.63	38.95	77.48	901.22	135.23	878.01	162.12
Propithecus_perrieri	279.14	246.64	93.91	71.91	1285.59	305.73	176.05	129.68	258.45	234.41	258.45	227.82	1373.18	312.95	19.50	92.86	824.18	77.77	819.95	83.18
Propithecus_tattersalli	166.10	251.10	92.35	71.35	1358.19	309.41	180.95	128.46	264.19	235.59	264.21	231.30	1411.90	273.59	29.72	76.28	758.02	116.27	742.26	121.06
Propithecus_verreauxi	202.00	243.65	136.96	63.75	2687.26	336.73	123.74	212.99	271.94	208.64	272.30	205.14	643.38	165.32	4.86	101.63	424.73	18.95	393.26	23.97
Varecia_rubra	388.80	223.48	85.68	62.34	2052.55	292.28	156.22	136.06	245.82	212.64	247.22	194.88	2448.50	338.68	72.67	43.89	973.97	278.16	960.71	422.91
Varecia_variegata	868.17	200.53	106.17	65.03	2372.39	279.65	117.60	162.05	225.98	177.52	226.22	167.38	1828.06	337.82	43.35	72.30	934.70	162.11	928.13	196.57
Alouatta_belzebul	180.14	259.09	108.73	79.09	429.87	329.54	191.68	137.85	255.72	260.29	264.29	253.63	1950.96	336.36	22.94	69.78	934.05	91.07	229.68	693.81
Alouatta_caraya	399.98	237.95	123.70	66.12	1791.20	325.17	137.78	187.39	249.49	216.53	256.65	212.34	1427.09	238.91	22.23	64.92	652.47	83.31	422.20	111.79
Alouatta_guariba	530.28	200.42	110.11	59.84	2477.26	288.70	105.12	183.58	217.35	179.28	229.50	167.06	1414.66	195.55	61.45	40.67	532.46	212.83	473.74	234.87
Alouatta_macconnelli	241.09	259.61	95.21	81.75	523.02	322.47	206.60	115.86	255.23	263.87	266.06	253.01	2287.94	360.22	69.03	51.15	970.61	244.37	320.77	747.83
Alouatta_nigerrima	93.80	266.36	96.34	75.18	435.84	332.43	203.70	128.73	261.92	267.36	271.96	261.34	2236.30	318.25	55.22	50.26	909.33	203.60	318.43	779.18
Alouatta_palliata	439.61	242.21	97.83	70.90	1028.33	313.46	176.15	137.31	244.12	241.38	254.03	227.61	2187.24	352.48	39.77	62.18	931.31	147.84	477.72	387.71
Alouatta_pigra	215.49	251.08	106.90	65.08	1788.14	330.69	167.76	162.93	262.42	245.96	269.51	225.20	1715.48	285.55	42.68	58.59	738.92	146.24	455.22	222.77
Alouatta_sara	324.01	250.13	112.99	67.80	1413.85	326.05	160.24	165.81	260.77	230.91	262.98	228.76	1827.39	293.32	44.68	56.59	800.09	158.89	591.59	182.00
Alouatta_seniculus	397.35	250.82	97.93	82.69	493.24	311.21	193.07	118.14	248.33	250.73	256.11	243.61	2555.72	315.38	105.92	33.80	876.04	370.23	522.59	683.80
Aotus_azarae	303.70	240.40	127.46	60.41	2911.94	339.82	129.21	210.60	268.99	206.65	272.24	199.64	863.83	131.79	16.78	56.50	363.61	70.33	336.20	91.78
Aotus_griseimembra	419.54	258.88	103.17	83.35	446.45	321.41	198.01	123.40	256.71	257.75	263.69	252.53	2018.88	301.99	41.55	52.29	778.95	168.35	414.68	537.85
Aotus_infulatus	248.74	255.95	118.73	74.52	675.16	334.54	173.83	160.71	255.47	251.25	262.97	246.55	1913.31	326.61	16.72	70.97	909.32	70.99	328.90	458.32

Aotus_lemurinus	2295.71	153.50	96.95	85.39	351.42	211.06	97.82	113.24	152.07	153.06	157.15	148.45	1896.75	251.15	71.93	36.03	660.30	263.52	464.11	540.78
Aotus_nancymaae	289.47	254.67	102.79	82.66	423.92	315.32	191.53	123.79	254.91	249.51	258.93	248.39	2323.25	268.60	102.21	28.21	752.08	352.14	585.77	415.55
Aotus_nigriceps	193.39	256.05	107.68	75.54	519.44	325.88	182.97	142.91	255.74	251.33	261.56	248.75	2166.56	312.03	43.08	53.91	883.43	163.65	446.39	360.11
Aotus_trivirgatus	233.96	262.77	99.91	84.55	469.00	325.04	207.27	117.78	257.17	266.11	268.14	256.56	2398.68	374.08	81.49	50.36	1021.93	278.68	362.54	898.59
Aotus_vociferans	197.19	258.30	93.08	84.06	490.60	315.08	204.76	110.32	255.24	260.34	263.42	250.95	2906.62	332.04	153.15	23.85	939.40	512.15	576.80	823.39
Ateles_belzebuth	305.59	256.44	99.64	83.86	514.22	318.07	199.69	118.38	251.85	258.48	261.86	248.86	2729.62	348.26	115.58	33.57	974.34	405.11	493.62	867.69
Ateles_chamek	194.51	255.27	110.42	74.49	680.00	327.05	177.87	149.18	256.86	247.70	262.01	245.35	2106.31	305.96	45.48	53.81	859.21	170.59	471.01	314.34
Ateles_fusciceps	500.70	243.57	90.58	85.17	366.15	298.78	192.73	106.05	242.62	243.59	248.11	238.88	3277.87	422.50	127.47	44.59	1162.53	438.61	770.99	888.05
Ateles_geoffroyi	315.11	247.27	91.71	74.03	743.90	311.80	188.62	123.18	246.13	248.07	256.46	237.31	2566.90	416.91	41.76	62.83	1093.87	158.47	475.74	580.17
Ateles_hybridus	539.91	251.19	103.78	83.43	444.34	313.42	189.38	124.04	249.28	249.21	255.72	244.70	2153.21	319.09	46.61	49.55	816.14	191.35	478.95	551.10
Ateles_marginatus	252.55	254.90	120.36	73.07	515.00	338.90	173.07	165.83	251.05	252.67	260.89	248.80	2137.58	346.31	19.52	66.30	974.67	83.13	392.26	632.36
Ateles_paniscus	188.50	261.78	90.82	79.80	562.16	324.87	211.65	113.22	257.71	267.97	269.31	255.13	2203.47	355.02	64.66	51.94	940.14	229.54	260.33	706.22
Brachyteles_arachnoides	611.79	191.99	101.79	57.02	2484.79	273.71	96.87	176.84	221.37	159.32	222.12	158.87	1607.05	246.61	48.51	52.09	688.34	171.10	661.23	174.39
Brachyteles_hypoxanthus	521.41	216.58	115.11	63.59	1943.02	300.93	121.38	179.55	233.63	191.26	239.24	189.80	1241.55	228.34	21.11	69.10	625.90	74.03	468.59	83.84
Cacajao_ayresi	45.64	268.81	98.45	89.57	327.63	324.24	215.29	108.95	263.97	271.15	271.72	263.76	2356.49	339.69	112.34	37.07	915.58	369.27	413.19	903.88
Cacajao_calvus	191.19	261.17	105.86	80.92	476.68	324.34	193.93	130.41	261.97	255.04	265.73	253.97	2232.88	271.39	90.95	33.35	753.81	313.08	572.31	366.15
Cacajao_hosomi	244.47	259.88	103.37	89.76	396.21	319.11	204.59	114.52	254.29	262.20	263.17	253.70	2929.44	374.71	157.26	26.45	1005.55	526.76	574.84	937.80
Cacajao_melanocephalus	119.88	263.58	94.26	83.95	489.88	323.03	211.09	111.94	258.75	267.13	269.04	256.49	2959.25	364.74	138.39	30.42	1028.54	469.65	498.46	950.52
Callicebus_brunneus	216.29	253.99	113.30	71.72	689.43	330.63	173.48	157.15	255.30	246.21	261.22	244.06	2010.93	306.50	28.18	60.00	867.78	111.93	443.59	163.32
Callicebus_caligatus	45.50	267.88	88.62	80.74	388.96	325.29	216.09	109.20	263.14	269.75	272.79	263.09	2402.69	315.11	73.17	42.02	893.86	263.21	378.33	890.83
Callicebus_coimbrai	174.79	242.31	85.77	66.44	1537.92	307.55	179.50	128.06	234.67	248.82	258.40	220.00	1060.02	171.67	36.75	49.80	452.68	129.65	198.26	356.99
Callicebus_cupreus	159.62	258.42	102.10	80.92	442.32	319.30	193.44	125.86	259.11	253.05	262.81	251.80	2380.64	300.35	77.94	39.67	850.56	277.57	575.81	375.61
Callicebus_donacophilus	184.10	251.75	119.27	67.80	1405.11	331.56	156.92	174.64	262.57	232.87	264.03	230.63	1736.43	285.04	35.20	60.88	783.96	129.80	569.39	156.32
Callicebus_hoffmannsi	90.64	267.58	93.93	78.07	474.20	330.87	210.86	120.01	262.47	270.68	274.05	262.06	2210.23	323.38	63.00	51.95	922.14	218.56	268.42	904.86
Callicebus_lugens	251.32	260.28	99.34	83.49	537.81	323.06	204.54	118.53	254.58	263.35	266.03	252.50	2655.76	366.78	93.17	42.43	1020.48	342.61	421.11	917.43
Callicebus_moloch	254.79	254.79	120.62	74.67	493.01	336.52	173.81	162.71	251.81	252.46	260.40	248.61	2078.07	340.70	18.04	67.63	957.44	78.62	355.86	565.96
Callicebus_nigrifrons	725.43	208.81	119.09	65.13	1984.99	287.73	106.38	181.35	227.67	182.47	229.46	179.97	1422.43	266.82	19.41	73.34	717.29	70.65	617.43	86.96
Callicebus_personatus	454.73	224.37	113.11	65.60	1744.76	306.11	135.04	171.07	238.82	201.46	244.69	200.01	1144.02	205.18	23.88	65.82	566.79	84.01	398.69	91.83
Callicebus_torquatus	71.72	263.62	90.54	86.46	363.44	317.56	213.48	104.08	260.32	266.27	267.47	258.31	2824.63	337.46	156.62	26.10	942.51	495.90	525.12	849.77
Callimico_goeldii	249.73	256.44	104.89	80.34	564.92	319.08	188.35	130.73	257.46	251.21	261.65	247.75	2382.98	286.41	102.10	34.11	809.46	344.98	612.25	441.91
Callithrix_aurita	662.93	198.97	110.54	61.29	2142.03	280.42	102.02	178.41	220.93	170.21	224.48	169.78	1447.18	253.84	27.64	66.03	691.81	96.78	600.37	102.57

Callithrix_geoffroyi	384.74	230.87	106.39	66.55	1612.41	307.31	148.83	158.48	242.95	210.36	249.55	207.84	1100.52	184.96	31.53	57.95	506.08	111.70	353.85	118.90
Callithrix_jacchus	340.71	254.78	110.82	74.02	930.13	330.76	181.67	149.09	252.65	253.55	265.98	242.51	1015.36	210.61	5.52	87.66	554.98	23.82	133.81	215.32
Callithrix_kuhlii	377.52	227.72	86.05	65.50	1377.55	289.81	159.57	130.25	237.50	215.03	242.84	207.60	993.64	139.60	44.71	41.28	368.09	156.45	288.70	178.45
Callithrix_penicillata	600.87	235.31	121.25	69.50	1297.14	313.92	140.51	173.41	243.17	220.04	247.70	215.72	1393.92	263.96	8.56	79.46	711.14	33.58	387.64	77.85
Callithrix_pygmaea	170.95	258.46	100.22	81.11	483.74	318.97	195.45	123.52	258.35	254.78	263.29	251.21	2479.93	302.50	97.74	35.69	858.27	337.51	575.51	481.37
Cebus_albifrons	248.11	256.89	101.43	80.55	515.37	320.02	193.75	126.27	255.45	254.57	262.28	249.43	2425.47	318.30	87.54	41.36	890.38	305.99	511.38	575.09
Cebus_apella	189.10	257.99	105.20	76.00	622.55	329.24	189.55	139.68	256.37	256.89	265.07	249.78	2088.59	341.03	40.13	60.59	933.58	150.33	316.12	585.36
Cebus_capucinus	398.42	245.99	91.23	77.44	685.77	307.54	189.14	118.40	245.84	246.41	254.10	236.53	2819.61	399.14	81.06	50.87	1075.50	286.73	602.75	694.26
Cebus_kaapori	81.37	266.40	97.62	83.88	371.39	326.98	211.19	115.79	263.08	269.85	271.15	261.85	2068.09	394.27	30.85	75.03	1062.25	114.01	136.91	903.39
Cebus_libidinosus	433.42	248.37	121.63	71.39	1040.93	328.91	159.11	169.81	251.31	239.22	258.82	233.13	1388.00	258.42	6.66	80.56	702.33	29.37	310.86	124.72
Cebus_olivaceus	259.42	259.27	96.60	79.85	561.69	324.51	203.94	120.57	254.86	262.74	266.35	252.31	2083.04	340.85	50.93	57.50	921.72	185.30	283.98	683.76
Cebus_robustus	397.35	230.34	106.91	66.69	1610.77	306.91	147.97	158.94	242.36	209.82	248.89	207.25	1098.95	185.39	31.27	58.27	506.33	110.40	354.78	117.84
Cebus_xanthosternos	525.15	229.66	107.89	69.79	1416.85	303.63	150.78	152.85	236.93	216.62	243.66	208.53	818.80	143.09	17.91	65.63	378.98	65.69	256.48	107.65
Chiropotes_chiropotes	250.34	260.30	96.66	82.14	523.69	324.09	206.90	117.18	255.37	265.13	266.83	253.79	2275.62	364.63	68.23	52.56	981.04	239.95	308.98	787.53
Chiropotes_utahicki	209.17	257.82	114.54	79.57	373.08	331.11	186.74	144.37	255.45	257.46	262.14	252.87	2010.98	330.22	22.77	67.11	925.29	93.16	281.12	631.35
Lagothrix_cana	374.47	248.18	108.64	76.04	544.48	317.62	174.27	143.35	248.07	242.99	253.87	240.48	2167.60	310.43	45.94	53.36	879.58	172.79	454.33	386.35
Lagothrix_lagotricha	170.67	260.16	93.28	82.59	556.33	318.81	206.20	112.61	256.55	262.80	266.04	251.84	3032.40	356.01	142.81	27.23	1009.82	497.87	561.78	892.61
Lagothrix_lugens	910.64	231.66	98.88	84.26	457.84	293.08	175.98	117.11	228.14	233.94	237.21	225.35	2465.69	341.57	62.38	42.98	908.77	256.82	425.70	815.10
Lagothrix_poeppigii	222.39	256.97	100.69	83.22	438.73	316.66	196.09	120.56	256.51	253.36	261.31	250.41	2503.96	281.55	123.36	25.40	793.42	415.79	618.81	506.85
Leontopithecus_chrysomelas	220.21	234.74	77.24	64.56	1251.26	292.05	173.38	118.67	243.52	225.44	248.90	216.66	1167.11	144.90	61.59	28.81	382.35	213.07	319.59	247.35
Leontopithecus_chrysopygus	576.39	202.97	119.46	61.71	2530.10	289.97	98.15	191.83	231.72	172.04	231.77	168.04	1261.38	198.30	37.51	51.57	545.96	139.56	539.38	160.28
Leontopithecus_rosalia	52.60	228.54	79.02	57.30	1868.70	296.19	159.50	136.69	243.32	204.97	253.45	204.96	1064.63	156.78	37.93	41.58	410.59	120.50	350.68	120.70
Callithrix_argentata	106.68	261.28	96.30	82.45	467.31	322.55	206.36	116.19	256.95	265.65	267.52	255.76	2036.92	343.47	43.07	63.82	949.04	153.26	185.57	864.60
Callithrix_emiliae	340.28	249.95	139.15	70.01	661.06	348.45	150.59	197.86	247.48	243.78	256.55	241.23	2162.84	357.44	5.91	72.45	1019.42	37.82	475.78	439.80
Callithrix_humilis	94.45	267.78	94.19	78.42	476.93	330.98	211.21	119.77	262.47	270.84	274.28	262.09	2219.03	326.91	64.78	51.57	925.66	224.43	270.26	914.39
Callithrix_mauesi	102.72	266.56	96.22	73.82	403.29	332.55	202.18	130.37	262.48	266.63	271.78	261.93	2259.20	318.14	58.42	49.63	915.14	212.72	322.36	850.62
Callithrix_saterei	69.97	268.00	93.06	75.25	392.76	330.67	207.52	123.15	263.87	268.33	273.07	263.22	2258.78	303.37	67.40	44.25	867.97	251.29	336.24	852.77
Pithecia_irrorata	158.16	257.36	106.82	74.81	521.92	327.44	184.29	143.15	256.79	252.85	262.96	250.06	2167.85	315.13	39.19	55.33	894.97	153.05	429.66	367.99
Pithecia_monachus	163.12	259.35	98.30	83.10	449.17	317.63	199.67	117.96	259.16	256.22	263.76	252.56	2587.03	293.72	124.44	26.50	830.62	422.40	614.27	543.42
Pithecia_pithecia	162.39	263.11	90.14	79.74	560.93	325.83	213.35	112.48	259.13	269.28	270.62	256.48	2224.77	354.51	66.19	50.87	939.99	233.72	264.14	707.39
Saguinus_bicolor	61.40	271.21	84.82	81.68	440.74	326.90	223.68	103.22	267.22	275.70	277.42	266.48	2277.53	301.74	84.81	40.53	848.31	282.93	327.41	824.95

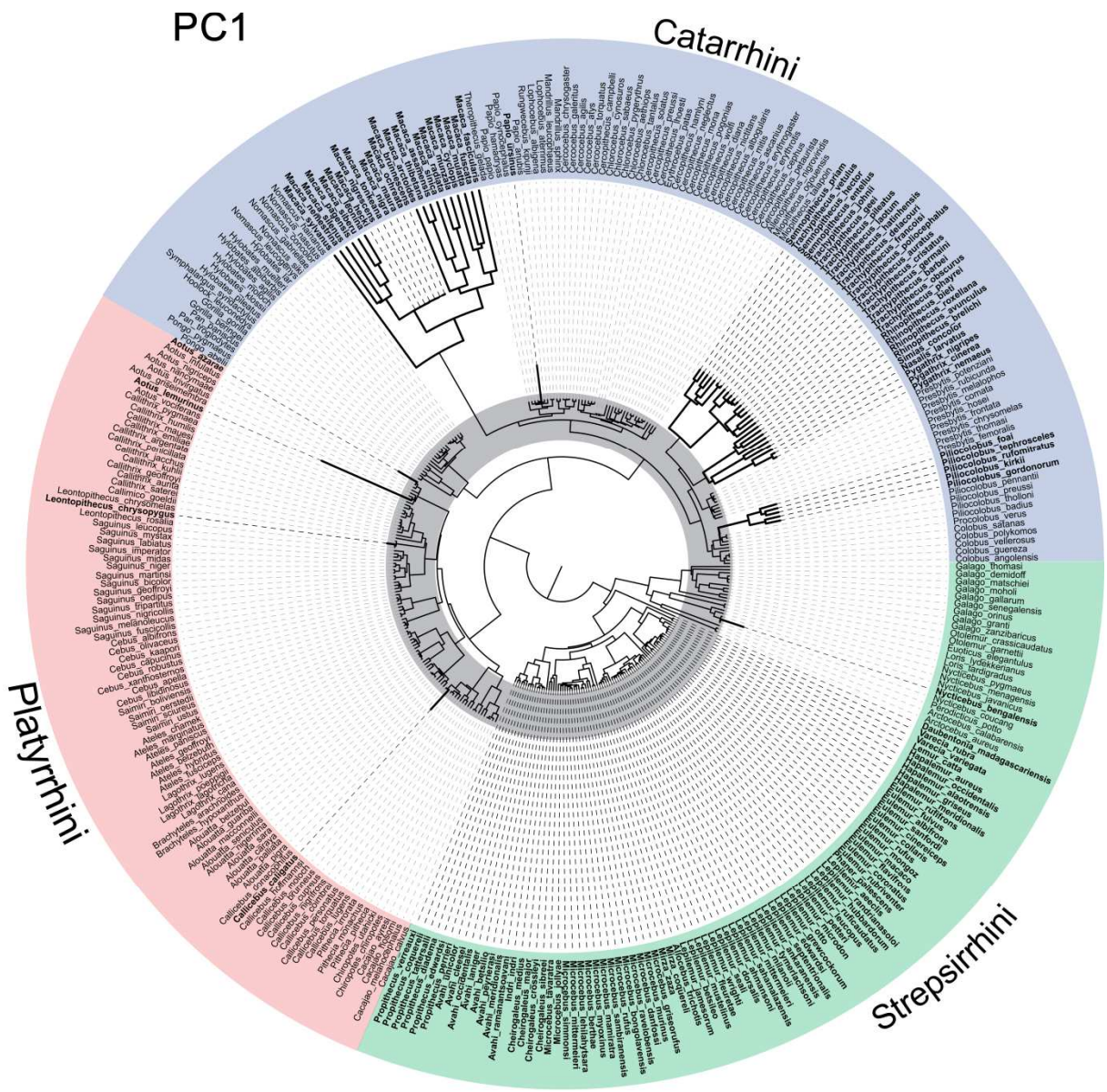
Saguinus_fuscicollis	242.95	256.06	99.28	82.90	431.45	315.50	196.25	119.25	255.24	253.50	260.57	249.76	2556.17	300.05	114.90	29.57	847.24	391.12	580.68	559.68
Saguinus_geoffroyi	190.91	257.39	82.57	83.97	380.59	308.67	210.82	97.85	254.29	258.86	262.26	252.37	4229.82	522.60	160.61	41.44	1424.03	548.52	800.40	1272.44
Saguinus_imperator	281.61	252.25	111.29	75.44	700.64	319.92	172.94	146.98	255.98	242.16	258.48	241.34	2021.90	278.10	41.73	51.80	797.68	156.02	605.42	196.97
Saguinus_labiatus	101.74	262.18	98.89	77.69	486.83	325.73	198.33	127.40	260.86	259.58	267.71	255.35	2275.11	307.16	58.87	48.53	873.51	215.70	441.85	474.57
Saguinus_leucopus	868.13	238.11	98.81	86.49	391.69	296.62	182.84	113.78	234.85	238.77	242.76	232.73	2907.68	402.30	70.75	45.21	1052.64	277.85	603.19	909.71
Saguinus_martinsi	73.81	271.97	87.95	80.60	575.89	333.42	224.94	108.48	266.73	279.84	280.10	265.87	2274.19	375.19	67.08	53.53	991.67	233.21	233.46	883.20
Saguinus_melanoleucus	242.46	255.88	105.24	77.75	540.97	318.57	183.93	134.64	257.92	247.93	260.93	247.49	2082.02	274.85	47.54	46.25	772.32	187.48	586.70	248.02
Saguinus_midas	176.31	262.56	91.22	79.37	572.94	326.81	212.44	114.37	258.28	269.61	270.31	255.83	2241.68	364.89	62.12	52.94	963.92	220.44	241.67	737.75
Saguinus_mystax	131.07	260.07	99.17	81.95	393.08	319.42	198.86	120.56	260.09	255.68	264.09	254.31	2490.56	305.32	91.07	35.43	862.94	320.17	575.58	425.99
Saguinus_niger	141.62	262.61	104.01	81.36	411.97	328.73	200.78	127.94	259.22	265.01	267.95	257.53	1975.29	352.82	27.88	71.61	968.43	106.60	169.74	789.27
Saguinus_nigricollis	257.38	254.73	93.24	83.68	523.41	311.00	200.13	110.87	252.10	256.57	259.94	246.69	2922.07	330.32	144.28	24.74	943.53	489.94	586.04	802.57
Saguinus_oedipus	158.99	267.72	97.45	82.01	389.87	329.59	210.78	118.81	265.17	269.41	272.89	263.01	2047.65	291.15	33.43	55.69	798.41	122.02	281.61	631.70
Saguinus_tripartitus	224.67	253.78	96.24	85.58	523.68	309.93	198.18	111.75	248.14	257.77	258.70	245.58	2927.09	316.38	177.25	18.74	903.95	548.08	627.49	832.50
Saimiri_boliviensis	521.64	243.32	113.01	75.98	790.21	313.52	164.40	149.12	247.29	232.65	250.74	231.36	2033.70	288.44	54.26	49.99	805.41	194.23	558.46	249.70
Saimiri_oerstedii	239.20	253.41	107.54	76.83	724.76	327.68	188.67	139.01	248.56	254.99	263.93	244.82	3376.50	589.81	44.73	62.35	1469.24	173.67	619.30	1053.58
Saimiri_sciureus	217.86	258.69	101.42	80.41	510.65	324.54	197.67	126.87	255.32	260.32	264.64	251.87	2379.59	343.36	76.06	48.49	947.27	267.71	385.90	716.30
Saimiri_ustus	159.81	255.46	108.97	73.11	521.42	329.64	179.83	149.81	253.63	252.29	261.34	248.55	2124.88	322.44	32.74	59.00	908.89	132.14	344.89	428.91
Allenopithecus_nigroviridis	387.49	250.21	99.84	84.98	510.84	312.05	195.11	116.93	246.88	248.23	256.70	243.76	1869.55	225.36	76.94	29.26	627.06	284.61	464.86	428.00
Cercocebus_agilis	584.53	243.31	109.74	78.79	643.92	316.89	177.35	139.54	239.24	242.89	251.52	235.42	1646.75	232.99	36.99	46.21	617.90	149.14	375.83	430.30
Cercocebus_chrysogaster	387.43	251.13	96.19	84.85	455.64	307.12	194.24	112.89	249.08	245.82	256.70	245.34	1770.65	225.85	44.45	39.15	635.35	192.81	480.73	211.46
Cercocebus_galeritus	26.50	271.40	92.00	70.10	1214.70	335.90	205.70	130.20	270.50	283.90	285.40	254.60	686.80	103.50	11.30	48.20	259.30	79.60	150.90	140.00
Cercocebus_torquatus	181.22	256.94	84.46	72.73	1023.09	318.87	203.21	115.66	249.71	256.24	268.62	242.03	2210.80	376.18	19.41	64.84	957.55	94.16	455.13	673.51
Cercocebus_atys	225.99	259.75	106.84	69.48	1092.72	340.70	185.70	155.00	254.38	259.58	273.78	246.14	2130.39	431.33	19.87	73.94	1065.29	100.72	317.19	753.16
Cercopithecus_albogularis	764.39	225.82	102.96	67.60	1529.02	305.58	154.65	150.93	232.11	215.73	243.12	204.46	943.28	202.77	16.72	72.10	445.76	70.88	229.97	103.09
Cercopithecus_ascanius	711.25	238.52	111.31	79.05	612.45	308.18	166.59	141.59	237.02	233.98	245.31	230.26	1571.35	219.28	33.22	50.35	592.28	135.09	398.05	261.08
Cercopithecus_campbelli	217.57	259.93	114.39	68.54	1089.70	346.05	177.90	168.15	251.25	258.38	273.88	247.01	2477.42	524.29	19.31	83.70	1308.65	96.07	316.12	973.58
Cercopithecus_cephus	464.50	242.82	96.69	76.69	807.40	307.01	181.45	125.55	242.33	235.15	251.57	231.26	1748.03	282.35	24.13	55.34	696.71	112.09	519.23	241.69
Cercopithecus_diana	192.65	258.81	99.36	72.54	941.01	331.66	194.97	136.69	255.21	260.71	270.09	246.20	2119.50	388.36	27.21	62.16	944.20	138.49	367.07	739.43
Cercopithecus_erythrogaster	56.00	267.41	82.57	73.29	1075.17	329.37	217.38	111.98	258.21	272.77	280.66	252.16	2032.66	350.09	19.96	65.59	887.00	93.78	322.37	802.46
Cercopithecus_erythrotis	321.81	251.45	86.70	74.86	878.55	315.76	200.47	115.29	239.89	255.68	261.92	238.95	2696.37	436.00	25.96	64.46	1217.90	117.55	404.85	1203.73
Cercopithecus_hamlyni	712.24	237.63	104.90	86.73	424.90	299.12	178.81	120.31	235.96	234.91	242.25	231.53	1819.91	221.19	68.89	32.26	607.15	253.35	504.49	346.62

Cercopithecus_lhoesti	813.93	233.37	107.23	86.52	396.09	296.20	172.86	123.34	231.52	231.26	237.62	227.76	1765.18	211.64	67.44	32.11	586.15	243.01	477.71	345.93
Cercopithecus_mitis	897.61	222.15	118.42	68.19	1516.73	306.44	128.63	177.81	230.17	204.34	238.05	200.16	1226.32	218.07	17.59	76.57	588.68	68.45	351.48	134.49
Cercopithecus_mona	301.69	261.11	102.88	69.57	1212.80	341.17	192.60	148.57	248.11	264.02	277.48	245.67	1618.37	284.59	10.08	72.82	752.89	49.55	235.43	728.60
Cercopithecus_neglectus	581.87	242.12	105.23	80.11	630.35	309.42	178.22	131.20	239.62	238.98	249.56	233.75	1707.53	239.85	39.73	45.95	636.00	161.34	439.01	342.65
Cercopithecus_nictitans	425.70	247.22	99.30	75.65	852.93	315.77	184.65	131.11	242.89	243.50	257.31	235.62	1781.48	288.75	23.46	57.53	731.30	105.78	436.90	433.62
Cercopithecus_petaurista	187.52	262.30	101.56	70.85	1052.78	339.22	195.68	143.54	258.30	264.28	275.72	248.67	1928.49	373.55	20.41	66.99	907.63	105.63	316.18	705.34
Cercopithecus_pogonias	539.68	242.57	102.22	79.14	678.70	309.15	180.41	128.74	240.56	238.40	250.27	233.22	1766.99	257.19	36.77	47.34	667.92	150.29	469.76	355.64
Cercopithecus_preussi	880.13	226.34	97.37	73.94	934.77	299.69	168.49	131.20	214.47	231.21	238.04	213.44	2327.88	396.10	16.83	68.80	1087.21	80.68	346.41	1074.02
Cercopithecus_solatus	377.77	249.49	96.75	74.39	987.77	312.94	183.60	129.34	252.30	233.57	258.05	233.57	1705.68	292.70	2.41	66.47	750.08	30.27	551.98	30.27
Cercopithecus_wolfi	406.08	249.72	99.39	85.53	483.04	309.36	193.78	115.57	247.11	246.70	255.71	243.48	1867.79	229.14	71.01	31.64	636.37	267.77	480.40	348.79
Chlorocebus_aethiops	1111.98	238.75	141.25	69.61	1644.96	344.33	140.58	203.75	235.30	230.67	260.09	218.31	848.73	187.22	6.60	92.91	472.34	29.86	135.20	318.94
Chlorocebus_pygerythrus	812.10	222.43	128.87	64.92	2230.43	318.40	116.23	202.17	239.60	196.47	246.89	190.74	744.28	158.72	6.23	88.13	406.03	26.13	253.12	43.37
Chlorocebus_cynosuros	990.46	221.99	131.43	65.84	1658.50	313.47	110.02	203.45	230.59	197.62	237.72	197.19	1163.21	216.20	2.88	86.69	582.98	19.35	338.61	30.16
Chlorocebus_sabaeus	269.94	269.94	132.40	61.95	1940.28	374.71	160.08	214.63	262.54	258.32	296.31	246.32	1123.59	276.80	2.55	107.26	691.76	16.44	152.93	260.25
Chlorocebus_tantalus	536.71	259.14	132.12	66.98	1585.52	359.69	158.73	200.95	250.34	250.46	281.11	240.63	1102.41	220.44	9.25	91.18	572.12	39.26	179.79	309.36
Colobus_angolensis	737.65	236.03	116.59	77.82	684.62	308.42	156.18	152.24	235.77	228.43	242.86	226.28	1586.60	226.50	29.13	54.75	615.36	120.59	419.77	190.60
Colobus_guereza	924.40	232.87	124.19	75.43	921.92	318.89	152.90	165.99	228.39	230.25	245.07	221.90	1351.77	227.35	20.17	65.11	596.92	85.33	277.38	387.94
Colobus_polykomos	259.72	257.91	115.96	68.80	1097.79	344.70	174.59	170.10	249.39	256.04	272.28	244.94	2375.44	488.64	19.61	78.55	1220.43	98.13	321.27	879.44
Colobus_satanas	467.77	241.20	93.99	76.40	847.23	304.01	181.79	122.22	240.30	233.78	249.90	228.70	1863.05	330.98	22.07	60.70	778.47	106.63	551.73	233.01
Colobus_vellerosus	194.42	266.86	101.41	70.36	1197.80	345.34	201.59	143.75	261.08	269.82	282.58	250.75	1252.96	224.68	12.23	64.33	542.56	68.27	250.84	422.14
Erythrocebus_patas	462.24	267.80	139.23	62.97	2146.39	377.26	153.36	223.90	264.00	252.32	295.65	240.28	842.55	194.99	3.59	111.91	491.52	16.87	124.32	214.85
Gorilla_beringei	2370.82	148.13	108.74	90.77	224.33	208.18	88.97	119.21	148.21	146.59	149.95	145.00	1557.26	207.59	35.51	38.54	540.54	172.74	433.72	337.28
Gorilla_gorilla	440.93	243.18	96.45	76.67	821.32	307.28	181.99	125.29	242.99	235.00	251.99	231.34	1761.01	286.86	25.00	55.32	704.67	116.09	528.78	238.40
Hoolock_leuconedys	943.89	204.85	112.15	47.03	3711.45	300.46	64.50	235.96	237.69	157.57	242.04	149.71	1804.80	372.06	8.26	87.65	1029.74	40.01	847.35	44.17
Hylobates_agilis	236.75	257.19	92.92	88.07	317.86	310.65	205.74	104.92	254.57	256.27	260.91	253.20	2633.63	326.76	117.80	31.55	898.91	394.67	665.07	745.06
Hylobates_albibarbis	137.38	261.17	83.50	88.39	329.03	310.93	216.87	94.06	259.09	262.55	264.10	256.11	2969.48	331.12	150.47	24.52	930.84	494.21	637.22	875.32
Hylobates_klossii	78.47	265.94	89.02	89.21	269.43	315.90	216.60	99.29	263.23	266.68	269.55	262.80	3437.89	412.88	203.65	24.65	1167.41	631.60	745.15	994.96
Hylobates_lar	426.60	250.33	104.77	64.83	1528.79	331.36	160.46	170.90	253.78	233.73	267.34	228.10	1837.92	319.38	41.84	65.68	831.03	153.03	442.72	292.87
Hylobates_moloch	546.41	238.36	94.09	82.03	396.90	293.76	179.73	114.03	238.17	233.99	241.81	232.60	3212.26	426.60	115.99	41.61	1194.03	386.85	855.68	580.06
Hylobates_muelleri	298.35	253.12	77.01	89.08	271.35	297.86	211.69	86.17	251.76	252.73	255.76	249.35	3034.90	343.55	170.54	21.41	944.99	563.31	738.74	795.71
Hylobates_pileatus	176.93	266.24	93.65	59.35	1407.18	340.52	182.73	157.78	266.92	249.70	283.53	245.99	1782.46	352.82	5.59	79.88	917.71	38.69	338.55	76.64

Lophocebus_albigena	606.64	239.63	102.75	79.79	633.08	305.96	177.73	128.23	237.63	235.81	246.77	230.96	1713.96	249.66	37.46	46.63	642.60	152.35	453.78	330.42
Lophocebus_aterrimus	454.05	247.43	102.11	83.89	508.04	307.72	186.09	121.63	245.56	242.91	253.35	240.50	1795.97	228.46	55.96	37.54	628.62	219.43	490.41	280.51
Macaca_arctoides	858.09	206.44	98.85	47.11	3741.83	297.51	85.12	212.39	240.93	158.95	247.09	152.81	1768.91	364.40	15.23	82.03	975.35	64.08	776.37	85.82
Macaca_assamensis	1627.98	163.47	106.56	44.88	4436.22	265.09	28.14	236.96	208.53	108.65	213.00	101.01	1520.24	323.43	12.10	86.94	859.62	52.42	740.66	61.03
Macaca_brunnescens	149.41	262.51	79.85	75.51	613.72	315.96	210.97	104.99	264.10	258.69	268.79	253.35	1863.85	235.62	38.17	43.73	657.87	159.32	391.35	390.68
Macaca_cyclopis	925.69	182.67	74.24	42.91	3596.24	261.35	88.82	172.54	220.97	153.33	222.98	133.35	2489.83	455.38	43.90	71.37	1236.95	155.36	1178.03	216.54
Macaca_fascicularis	257.74	256.44	88.91	75.53	824.23	317.70	194.36	123.34	255.94	249.53	265.85	244.73	2458.82	367.97	84.18	51.02	993.56	287.72	570.32	495.03
Macaca_fuscata	493.35	123.32	84.90	26.89	7963.21	281.99	-27.92	309.92	208.11	44.17	226.01	22.39	1988.86	293.77	76.49	42.97	769.80	254.35	723.55	281.79
Macaca_hecki	434.19	247.01	83.74	83.25	348.12	299.99	199.92	100.06	245.27	247.05	250.11	242.73	1896.10	215.81	107.73	19.80	583.10	362.96	444.60	520.38
Macaca_leonina	594.62	232.29	104.20	51.51	2719.92	319.71	116.53	203.18	250.70	197.76	260.42	191.92	1899.01	398.25	8.17	85.86	1063.85	41.37	676.52	60.64
Macaca_maura	564.03	236.31	86.21	74.99	390.33	293.99	179.62	114.37	235.52	234.80	239.72	230.80	2782.29	450.16	64.66	53.71	1211.49	234.26	556.65	347.48
Macaca_mulatta	977.32	191.99	113.26	39.57	5672.84	325.37	39.06	286.31	229.70	143.56	259.06	113.52	1134.28	253.59	11.00	94.12	659.89	46.21	444.45	62.37
Macaca_munzala	3241.97	87.25	130.46	45.89	5340.69	203.02	-78.66	281.68	151.40	15.16	151.40	15.16	881.97	198.18	2.49	97.82	542.62	12.51	542.62	12.51
Macaca_nemestrina	258.17	255.61	84.91	87.34	343.23	306.01	208.93	97.07	253.22	255.43	259.28	250.85	2805.20	338.28	139.89	27.88	927.11	466.60	665.71	776.59
Macaca_siberu	81.76	265.69	90.32	89.48	269.96	316.10	215.51	100.59	263.04	266.38	269.40	262.54	3471.33	406.66	213.97	22.79	1156.60	662.14	763.34	979.65
Macaca_nigra	423.32	242.87	83.44	84.13	298.43	294.91	196.48	98.43	240.10	243.85	245.11	238.21	2424.32	298.06	103.69	29.36	810.98	359.24	457.73	757.70
Macaca_nigrescens	485.94	242.76	85.93	84.20	275.34	295.90	194.36	101.54	243.29	242.29	245.07	239.41	1837.18	203.72	88.58	21.58	558.65	313.06	446.78	472.94
Macaca_ochreata	450.84	246.70	80.40	77.39	591.22	301.08	197.80	103.28	246.52	246.93	252.60	237.50	2183.97	277.07	88.79	31.56	751.93	317.19	389.90	542.17
Macaca_pagensis	72.45	266.39	86.65	88.73	268.45	315.53	218.61	96.92	263.56	267.21	269.83	263.27	3376.75	424.23	184.77	28.04	1187.17	575.75	711.89	1022.95
Macaca_radiata	431.84	263.75	103.92	54.71	2271.19	362.90	171.93	190.97	258.29	252.21	294.66	235.03	1213.47	352.21	3.58	96.89	785.41	18.93	181.99	233.54
Macaca_silenus	651.02	239.40	81.93	60.97	1239.88	308.77	175.08	133.69	232.86	238.49	258.03	226.46	3093.81	978.05	10.14	102.29	2122.17	49.54	309.66	1437.38
Macaca_sinica	200.44	262.85	75.50	69.47	1061.06	318.23	209.99	108.24	253.70	269.85	274.10	247.62	2015.60	356.42	45.71	62.70	900.87	208.46	380.14	622.04
Macaca_sylvanus	1420.56	132.24	133.67	40.37	6311.60	316.31	-9.28	325.59	79.95	216.19	217.74	56.09	586.67	90.78	6.21	54.76	252.24	31.51	38.12	235.26
Macaca_thibetana	1322.55	136.68	93.01	31.27	6976.96	276.96	-15.57	292.54	196.96	51.72	221.66	42.21	1242.75	221.88	26.28	68.77	599.86	95.20	524.20	108.02
Macaca_tonkeana	764.38	228.42	80.17	79.07	470.45	282.00	180.99	101.01	228.98	227.54	232.70	221.61	2189.48	279.75	98.57	30.53	751.79	341.19	483.77	486.87
Mandrillus_leucophaeus	388.15	249.24	88.44	74.79	879.90	314.86	197.12	117.73	237.84	253.49	259.73	236.77	2629.60	424.41	23.32	64.91	1191.42	110.63	392.93	1171.53
Mandrillus_sphinx	407.57	242.99	91.64	73.42	988.36	305.34	180.98	124.37	244.07	231.77	252.68	227.82	1898.55	338.50	15.34	64.46	800.88	79.31	593.41	161.37
Miopithecus_ogouensis	426.11	242.35	93.53	74.04	965.08	305.70	179.93	125.77	243.87	231.04	252.02	227.67	1796.22	312.74	17.52	62.15	745.02	85.87	576.30	168.59
Miopithecus_talapoin	582.48	238.27	101.31	69.78	1118.54	301.04	156.92	144.12	245.70	221.37	249.14	221.04	1269.35	217.41	4.58	72.47	536.06	31.37	492.74	36.62
Nasalis_larvatus	161.60	260.07	79.59	88.76	297.10	306.90	217.55	89.35	258.29	260.44	262.77	255.74	2909.95	330.01	154.45	23.17	914.53	508.82	673.40	815.59
Nomascus_concolor	1386.77	184.08	105.33	48.84	3547.24	273.03	61.05	211.98	219.25	137.91	221.56	132.43	1552.91	348.48	9.66	87.32	878.67	52.26	804.92	59.38

Nomascus_gabriellae	517.69	239.34	94.51	58.41	1648.35	315.60	154.28	161.32	244.57	219.46	258.09	215.74	2189.11	456.52	9.07	84.52	1212.61	47.85	545.72	92.95
Nomascus_hainanus	318.12	235.12	77.88	43.88	3473.50	311.00	135.50	175.50	260.25	184.88	273.00	184.88	1318.25	265.62	12.00	81.12	690.62	43.38	467.38	43.38
Nomascus_leucogenys	999.58	206.25	107.63	51.85	3212.50	292.21	86.62	205.59	236.89	162.59	238.94	158.98	1664.61	363.76	10.45	88.07	960.67	49.48	823.28	52.04
Nomascus_nasutus	575.30	206.76	83.44	37.23	5063.00	307.25	85.72	221.53	263.24	142.91	263.24	134.88	1467.88	282.79	18.73	81.69	820.58	74.47	820.58	76.55
Nomascus_siki	626.23	223.65	89.52	48.35	2977.72	301.07	117.96	183.11	246.30	185.40	255.19	180.15	2136.69	483.95	17.28	89.83	1245.20	71.53	865.49	85.62
Pan_paniscus	428.66	248.60	100.97	86.01	480.05	308.89	192.13	116.76	246.18	245.88	254.48	242.26	1885.72	231.41	74.57	31.09	639.83	277.89	486.02	358.07
Pan_troglodytes	473.61	243.27	96.34	75.79	852.12	309.24	182.54	126.70	241.00	237.72	252.74	231.20	1804.04	297.20	22.41	58.38	749.30	104.75	479.09	372.52
Papio_anubis	651.58	254.46	134.26	68.00	1629.17	355.34	153.74	201.60	249.47	244.23	276.27	234.42	970.38	200.99	8.61	94.37	508.64	36.69	169.63	247.50
Papio_cynocephalus	868.50	229.03	121.92	66.84	1489.84	315.65	131.96	183.69	236.81	210.36	244.35	207.15	1079.48	214.59	3.48	90.00	564.69	19.36	317.27	29.54
Papio_hamadryas	1074.29	237.07	130.11	63.07	2352.25	339.14	133.73	205.41	250.96	223.42	265.32	205.98	391.94	88.62	4.02	78.84	199.22	23.53	126.86	43.00
Papio_papio	171.99	276.14	136.52	58.23	2371.72	388.82	154.98	233.84	274.93	262.82	306.93	245.87	1054.07	306.46	0.33	128.37	759.67	2.22	97.24	183.51
Papio_ursinus	983.92	195.37	148.57	56.77	3727.75	313.29	51.93	261.36	225.43	150.83	236.00	142.60	513.65	107.10	5.01	84.69	290.64	18.97	212.69	24.22
Piliocolobus_badius	173.20	260.77	104.80	69.94	1070.25	339.35	188.00	151.36	256.68	260.58	273.99	246.77	1995.19	399.14	21.11	74.27	974.47	107.89	317.09	642.13
Piliocolobus_foai	1897.24	177.42	96.57	75.91	468.72	238.46	111.47	126.99	178.24	171.18	181.39	170.63	1609.03	236.31	12.51	58.40	622.38	67.58	298.83	140.65
Piliocolobus_gordonorum	1032.09	213.84	90.04	60.32	1556.12	285.83	138.44	147.39	221.83	195.21	230.30	190.35	1337.91	302.01	4.56	94.41	766.39	23.77	388.76	28.02
Piliocolobus_kirkii	28.47	273.10	89.08	67.45	1278.78	340.45	209.38	131.07	279.90	256.53	289.04	256.16	1582.05	395.92	42.56	81.59	880.52	150.71	304.71	151.03
Piliocolobus_pennantii	321.56	253.64	91.03	80.77	594.04	310.98	198.51	112.47	251.19	249.13	260.93	246.01	1911.46	276.48	25.10	49.02	728.98	125.89	497.05	369.44
Piliocolobus_preussi	352.93	250.99	85.86	74.15	898.97	315.08	199.95	115.12	240.27	256.14	261.21	238.05	2745.14	450.10	23.19	65.14	1263.09	112.42	392.93	1242.54
Piliocolobus_rufomitratus	643.95	241.56	108.71	81.91	531.51	311.67	179.23	132.44	237.60	241.96	248.12	234.83	1716.14	219.46	48.93	38.46	600.96	186.65	397.47	454.47
Piliocolobus_tephrosceles	1283.26	215.08	106.33	75.92	618.45	282.67	142.42	140.25	215.19	207.92	221.52	206.76	1118.43	195.19	8.95	70.19	488.45	41.22	267.75	63.28
Piliocolobus_tholloni	406.88	249.72	99.45	85.51	482.94	309.35	193.67	115.68	247.12	246.68	255.69	243.46	1866.25	229.07	70.57	31.79	636.42	266.41	480.11	346.80
Pongo_abelii	603.69	237.57	97.57	87.89	355.06	294.62	184.22	110.40	234.15	237.67	242.24	233.15	2622.73	305.39	125.81	27.71	870.53	436.87	674.94	738.14
Pongo_pygmaeus	208.16	257.77	81.15	88.53	312.98	305.94	214.66	91.28	255.89	258.59	260.70	253.08	2862.89	320.08	150.27	22.64	891.04	499.91	634.13	822.57
Presbytis_chrysomelas	171.68	259.80	82.60	88.99	328.35	308.39	215.99	92.40	256.22	261.07	263.40	254.91	3428.56	417.66	181.48	25.64	1154.85	605.83	737.34	1073.10
Presbytis_comata	669.59	230.82	95.10	82.34	383.02	286.15	171.32	114.83	230.94	225.88	233.98	225.32	3239.13	427.73	110.50	42.60	1206.46	370.37	908.56	526.99
Presbytis_femoralis	135.10	264.45	90.83	74.11	740.58	327.91	204.47	123.44	261.47	260.28	273.56	254.18	2330.10	364.37	61.76	53.26	979.65	229.33	501.15	522.72
Presbytis_frontata	331.86	250.09	77.50	90.03	239.51	294.25	208.49	85.76	249.10	249.43	252.13	246.78	3138.00	344.26	174.80	21.02	955.14	571.73	794.92	795.43
Presbytis_hosei	400.01	248.87	73.52	89.52	259.59	291.34	209.53	81.81	248.22	247.95	251.52	245.25	2910.79	316.72	179.81	17.09	868.89	591.97	727.01	711.26
Presbytis_melalophos	305.59	253.17	92.96	88.39	298.91	306.27	201.71	104.56	250.76	251.85	256.59	249.52	2652.69	327.55	116.37	32.26	905.19	388.69	677.67	737.36
Presbytis_potenziani	78.47	265.94	89.02	89.21	269.43	315.90	216.60	99.29	263.23	266.68	269.55	262.80	3437.89	412.88	203.65	24.65	1167.41	631.60	745.15	994.96
Presbytis_rubicunda	312.73	252.12	76.90	89.21	270.42	296.81	210.89	85.92	251.23	251.82	254.57	248.28	2934.26	324.58	164.48	21.17	897.09	536.51	716.48	751.08

Presbytis_thomasi	656.77	236.53	89.54	84.23	418.29	291.73	186.46	105.27	233.28	236.72	241.56	230.90	2384.57	286.04	112.14	29.61	807.86	383.39	591.05	657.40
Procolobus_verus	194.36	259.88	99.14	72.84	964.17	332.74	197.27	135.47	257.91	262.15	271.58	246.76	1836.82	323.61	25.65	59.15	776.30	131.40	348.40	598.58
Pygathrix_cinerea	684.24	228.84	97.03	56.32	1982.77	308.93	138.52	170.41	234.96	207.61	250.88	200.72	2174.11	441.09	16.45	80.26	1181.68	72.00	564.81	121.62
Pygathrix_nemaeus	520.21	233.03	89.54	50.38	2635.90	311.99	135.86	176.13	248.04	201.40	261.91	195.25	2337.56	533.79	19.24	89.15	1366.82	78.71	753.79	117.34
Pygathrix_nigripes	470.76	240.54	93.21	60.21	1496.05	316.02	162.01	154.01	242.80	225.06	257.80	219.24	1884.59	350.92	8.51	77.98	971.23	47.58	422.38	108.93
Rhinopithecus_avunculus	308.89	220.47	80.61	38.59	4652.79	315.77	109.28	206.49	272.52	164.14	272.78	156.15	1729.62	349.04	14.36	85.81	972.11	69.73	971.34	73.14
Rhinopithecus_bieti	3602.29	59.70	115.91	44.61	5187.83	172.13	-85.11	257.24	122.25	-0.69	122.25	-9.19	771.29	173.76	5.62	88.88	452.02	23.88	452.02	25.74
Rhinopithecus_brelichi	1298.07	125.75	74.64	25.86	7361.18	269.93	-13.71	283.64	198.61	27.04	217.39	27.04	1326.50	209.18	30.32	55.39	555.32	94.89	518.00	94.89
Rhinopithecus_roxellana	1741.67	102.07	99.11	31.14	7293.52	251.54	-59.73	311.27	185.57	3.62	193.26	3.58	893.53	171.24	6.98	78.47	469.34	26.85	440.25	26.85
Rungwecebus_kipunji	2030.75	162.00	103.25	62.50	1465.50	241.75	77.00	164.75	168.25	147.50	178.50	140.00	1938.00	393.50	7.00	87.00	991.00	42.00	549.50	53.00
Semnopithecus_entellus	312.14	258.03	110.35	40.95	4260.61	389.05	121.16	267.89	272.52	208.00	311.30	199.57	1321.01	353.65	3.34	115.07	917.00	24.15	251.64	31.31
Semnopithecus_hector	1005.68	197.10	108.88	43.52	4792.13	306.70	58.32	248.38	240.36	143.37	246.19	126.45	1857.21	506.41	6.20	110.13	1254.89	49.62	988.79	67.21
Semnopithecus_priam	332.10	269.61	96.99	56.27	2269.17	360.06	184.84	175.22	263.88	259.25	298.06	238.60	986.21	218.72	7.26	81.59	520.13	38.63	166.09	223.76
Simias_concolor	78.47	265.94	89.02	89.21	269.43	315.90	216.60	99.29	263.23	266.68	269.55	262.80	3437.89	412.88	203.65	24.65	1167.41	631.60	745.15	994.96
Symphalangus_syndactylus	431.67	246.13	94.44	87.63	334.31	300.65	193.60	107.04	243.74	245.05	250.13	241.95	2668.38	322.05	121.30	30.27	900.03	409.56	689.05	703.84
Theropithecus_gelada	2209.74	177.50	150.25	73.90	1300.59	278.89	76.81	202.08	175.55	165.65	195.00	162.26	936.02	270.55	8.23	110.70	618.35	32.90	190.21	166.78
Trachypithecus_auratus	339.38	248.65	97.25	79.00	491.52	309.24	186.55	122.69	248.12	243.99	253.58	241.76	2517.84	379.59	67.80	54.68	1046.62	240.12	641.01	452.73
Trachypithecus_barbei	424.20	247.13	102.57	56.54	1272.84	334.68	154.80	179.88	244.27	233.98	264.72	231.84	2602.22	538.09	2.96	93.53	1509.75	22.57	377.32	52.09
Trachypithecus_cristatus	263.67	255.27	84.17	88.40	302.28	304.35	209.53	94.82	253.24	255.09	258.41	251.13	2852.16	331.06	146.90	25.42	916.48	487.11	688.10	784.89
Trachypithecus_delacouri	179.72	232.38	74.79	37.79	4299.45	322.63	127.38	195.24	275.48	172.91	281.27	172.83	1748.94	368.90	11.75	86.71	992.64	60.40	840.99	60.40
Trachypithecus_francoisi	752.69	180.54	80.38	31.67	6188.45	302.61	49.43	253.18	245.54	98.84	253.50	94.69	1328.32	235.96	22.72	69.29	662.40	80.14	644.46	85.63
Trachypithecus_geei	639.41	212.97	94.16	44.91	4061.46	288.65	80.96	207.69	251.62	152.62	255.05	152.23	3282.59	771.71	7.55	98.82	2013.97	35.84	1674.28	35.86
Trachypithecus_germaini	274.78	256.72	92.21	59.09	1460.73	331.54	175.80	155.74	257.99	240.29	274.30	236.03	1887.33	372.47	7.16	80.31	992.58	42.72	394.70	94.45
Trachypithecus_hatinhensis	340.01	241.05	85.23	46.68	3047.61	319.70	139.20	180.49	260.32	204.47	274.45	197.10	2319.17	516.25	27.42	86.05	1327.93	101.39	828.99	125.05
Trachypithecus_johnii	938.15	225.28	81.75	62.17	1218.17	291.85	160.87	130.98	222.63	221.22	242.06	210.13	1903.81	441.88	19.45	74.03	984.41	84.78	331.69	290.98
Trachypithecus_laotum	577.54	228.14	98.60	50.98	2684.58	306.07	114.32	191.76	251.01	191.44	254.48	187.76	2469.01	626.73	2.82	105.04	1574.72	21.74	988.39	30.73
Trachypithecus_obscurus	200.45	259.49	91.43	75.64	731.21	322.50	200.11	122.39	255.67	256.40	268.45	249.34	2439.76	397.96	73.26	52.27	1051.38	264.39	496.48	571.96
Trachypithecus_phayrei	565.71	235.29	108.43	49.72	2887.39	329.64	113.52	216.12	254.57	199.38	265.18	192.46	1676.90	360.40	6.32	87.92	954.54	33.31	598.87	38.29
Trachypithecus_pileatus	574.67	223.49	96.67	45.61	3552.01	305.50	95.74	209.77	254.03	173.61	257.94	169.44	2313.49	494.19	7.39	87.97	1321.00	42.51	1056.13	45.11
Trachypithecus_poliocephalus	170.35	224.37	77.74	35.39	5182.48	322.46	105.61	216.85	281.15	167.39	281.48	151.85	1580.24	290.24	29.41	75.33	849.00	101.35	837.13	110.20
Trachypithecus_vetulus	245.85	260.88	78.23	68.20	1027.22	318.48	204.24	114.23	253.50	265.75	271.60	246.12	2097.02	344.50	55.48	58.06	882.50	235.51	478.30	569.00



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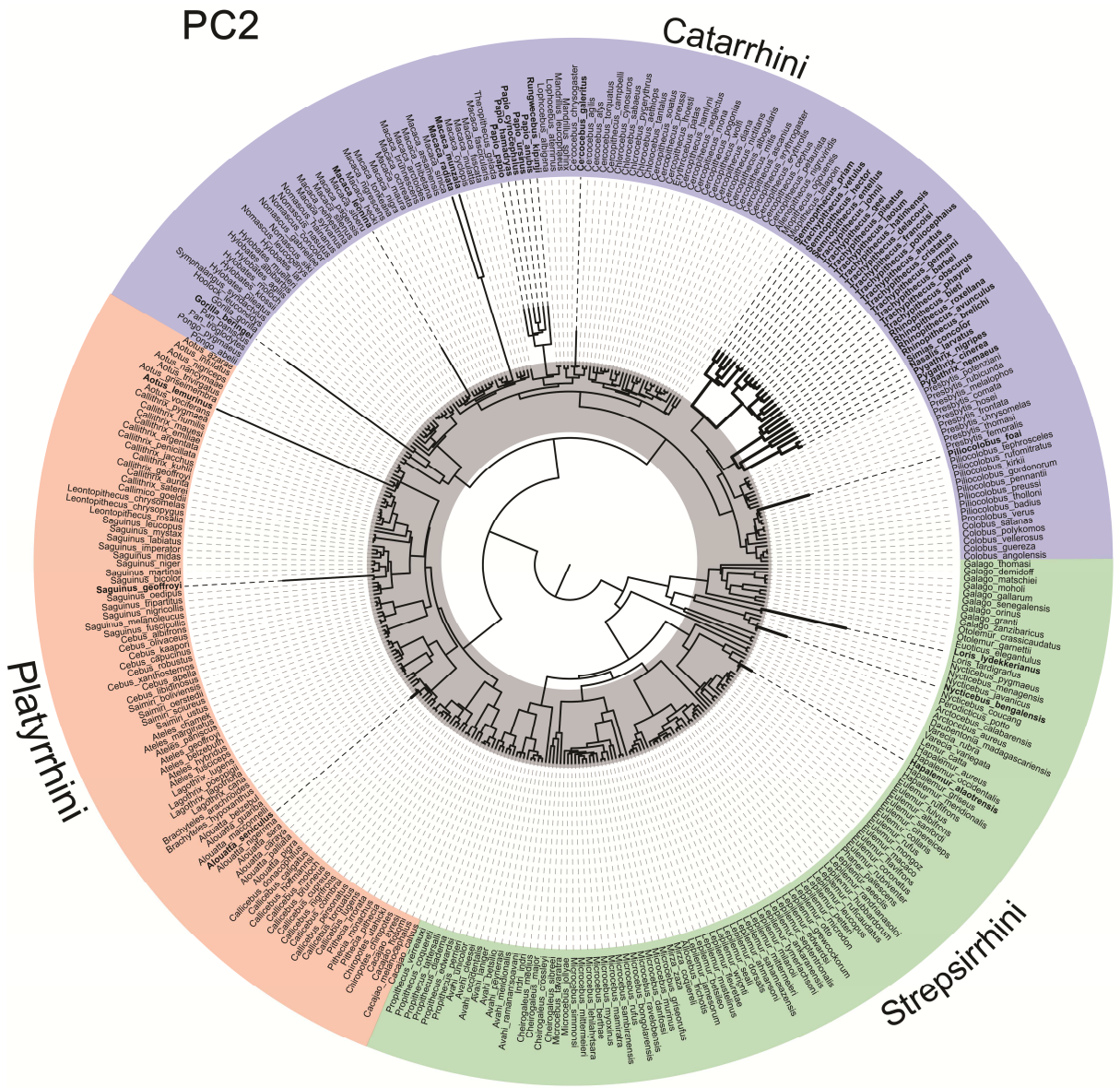

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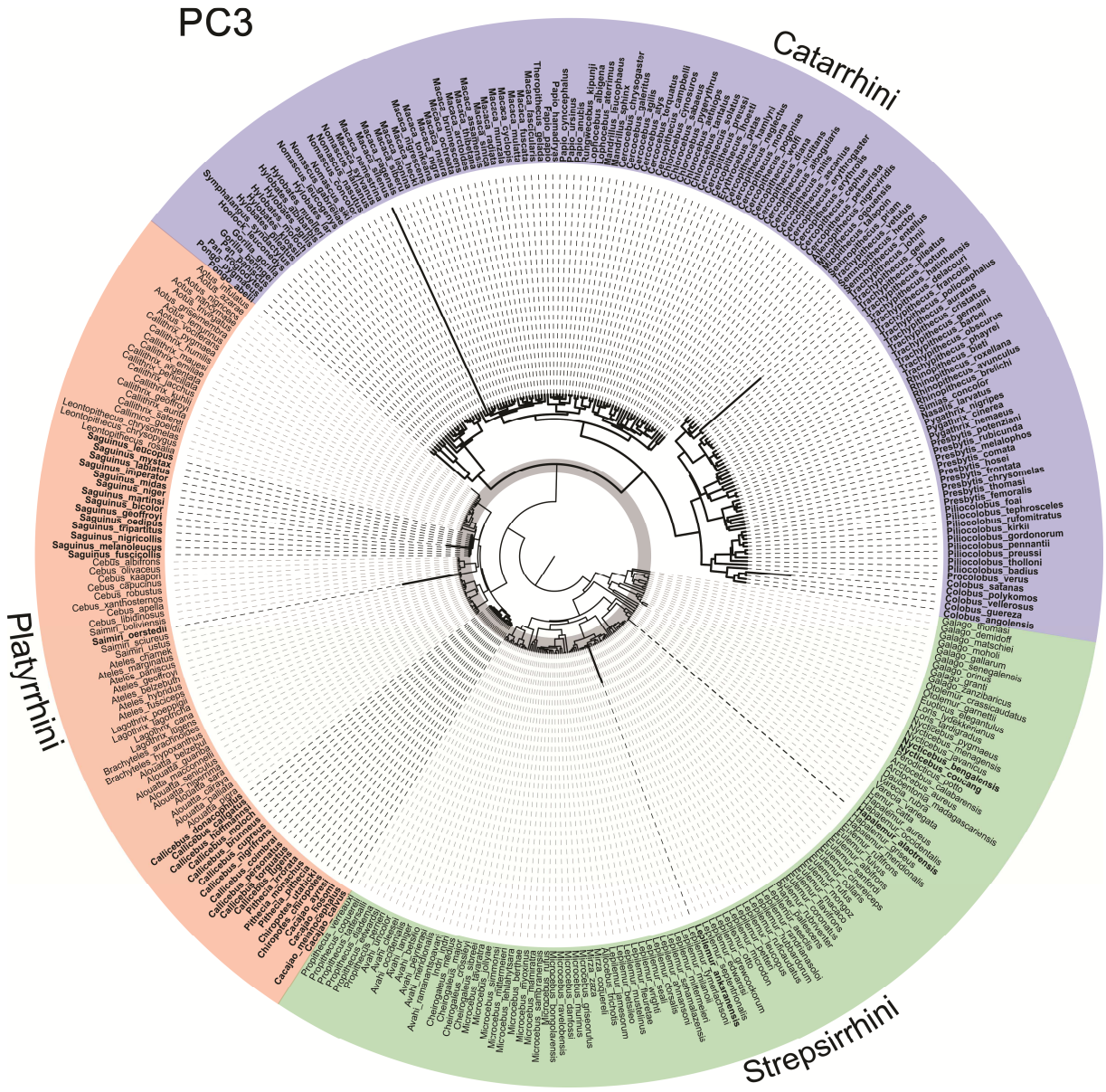

Figure S1. Shifts in rates of climatic niche evolution along the first three PC scores, based on the Models of Trait Macroevolution on Trees (MOTMOT; Thomas and Freckleton 2011) method, as implemented in MOTMOT package 1.0.1 (Thomas and Freckleton 2011). This method uses maximum likelihood to infer the number and the position on the phylogeny where changes in evolutionary rates occurred. MOTMOT analyses were run using the *transformPhylo.ML* function, using both algorithms (tm1 and tm2), with the maximum number of rate shifts set to 13 and without estimating the minimum clade size. Branch lengths are scaled according to the relative rates of evolution. Deviations from the background rate (grey region in center of the phylogenies) are highlighted in both species names (in bold) and in the black dashed lines. Branches that appear within the white circle in center of the phylogeny show decrease rates of climatic niche evolution, whereas branches that are beyond the grey ring show accelerated rates of climatic niche evolution. Notice that AUTEUR

estimates the location of the nodes where shifts would have occurred slightly earlier in the phylogeny than MOTMOT (see Figure 4). For instance, in the *Leontopithecus* lineage in PC1, AUTEUR identified the shift on the branch leading to *L. chrysopygus* and *L. rosalia*, whereas the same shift was identified in MOTMOT as only including *L. chrysopygus*. These situations occurred, in general, when the shifts comprised few species. When the shifts occurred in branches with more than four species, the results from both approaches tended to be more consistent with one another.

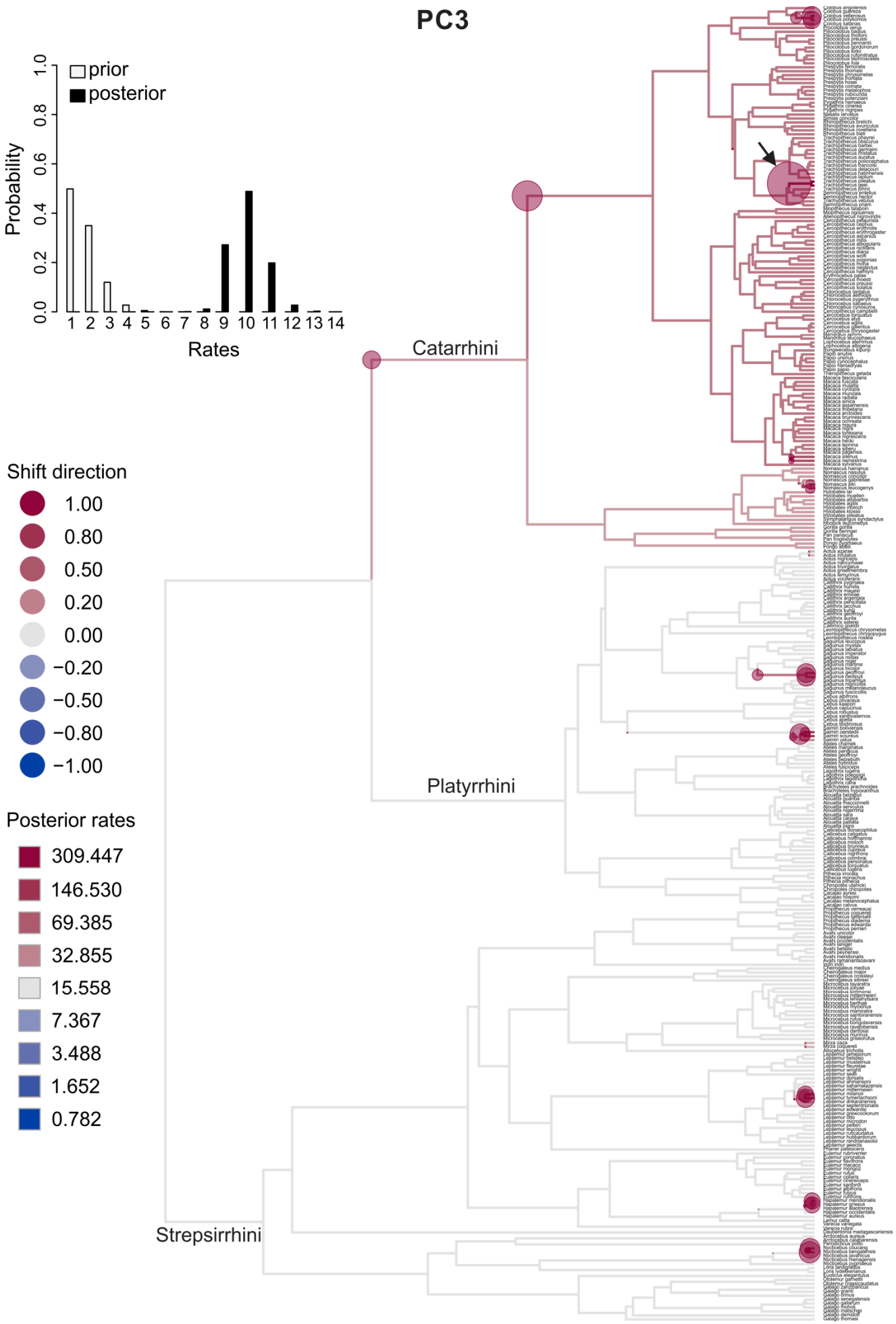
PC3
prior
posterior
Probability
0.0
0.2
0.4
0.6
0.8
1.0
1 2 3 4 5 6 7 8 9 10 11 12 13 14
Rates
Catarrhini
Platyrrhini
Strepsirrhini
Shift direction
1.00
0.80
0.50
0.20
0.00
−0.20
−0.50
−0.80
−1.00
Posterior rates
309.447
146.530
69.385
32.855
15.558
7.367
3.488
1.652
0.782

Figure S2. Posterior rate estimates of climatic niche evolution along the third PC, based on the AUTEUR method, indicating how the shift rates varied across the phylogeny. Background rates are shaded in grey, whereas background deviating rates are shaded in darker colors according to the posterior rates in the legend. Circles correspond to level of the support for each shift. Only one shift had high support and it is indicated with an arrow. See text for details.

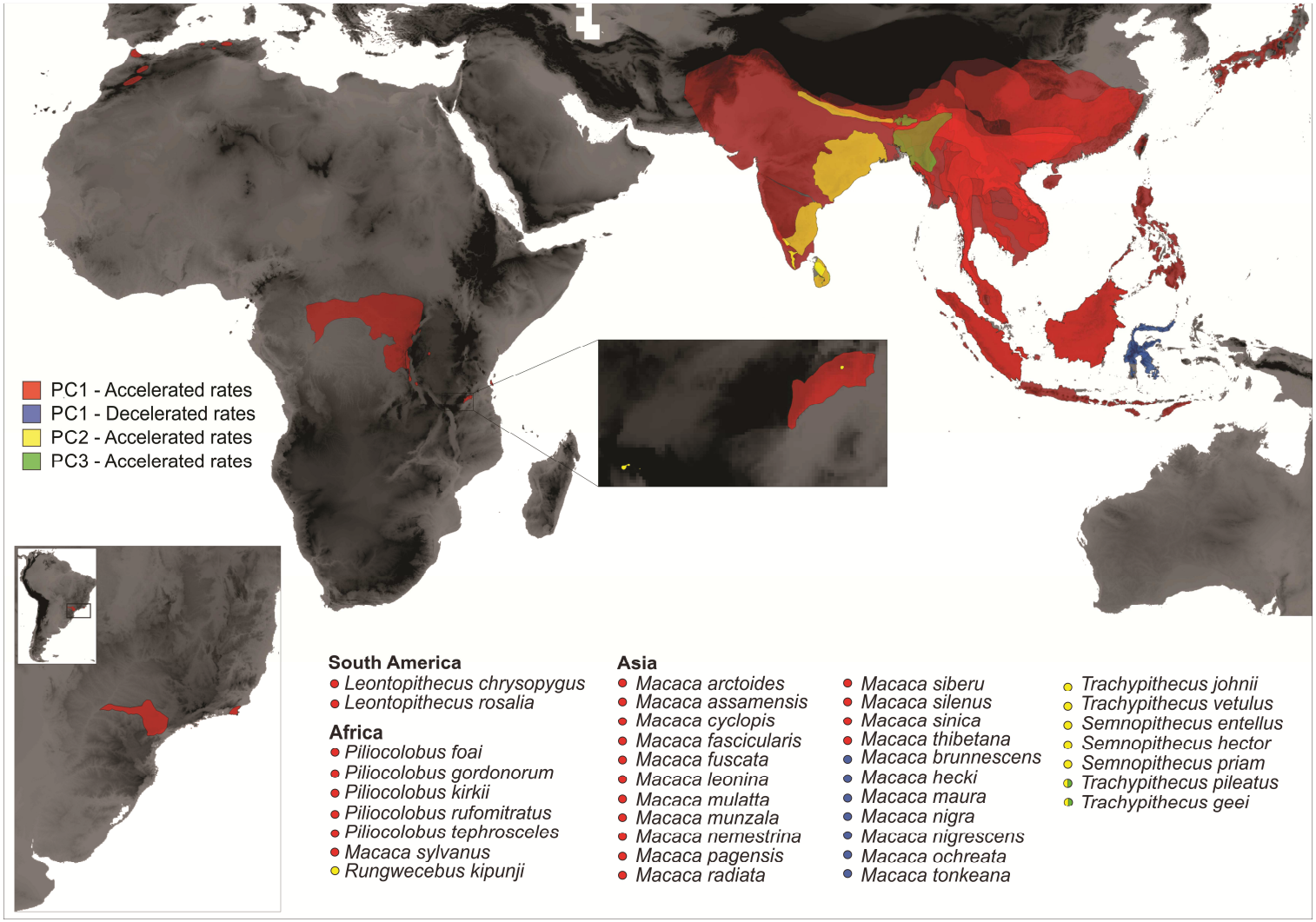

Figure S3. Geographical distribution of the species with high support rate shifts showed in AUTEUR analysis in Figure 4. Different shades of grey in the map on the background correspond to variation in altitude.

CONCLUSÃO GERAL

O estudo da dinâmica de nicho, através da análise do *tempo* e *modo* de sua evolução, permitiu identificar padrões a respeito de como os nichos climáticos mudam, tanto ao longo do tempo, quanto entre as principais linhagens de primatas. Ressaltamos a importância do clima na estruturação do padrão de distribuição das espécies, identificando que mudanças nas taxas evolutivas foram mais frequentes nos últimos 10 milhões de anos, o que coincide com mudanças no clima, particularmente uma diminuição da temperatura global. Isto sugere que a diversificação dos nichos climáticos dos primatas pode ter ocorrido em função do resfriamento da Terra, principalmente ao longo do Mioceno. Além disso, destacamos características gerais da evolução dos nichos climáticos em primatas: (1) a ocupação do espaço climático não foi homogênea entre as linhagens, com a maioria das espécies concentradas sob condições climáticas relativamente quentes e com moderada umidade (temperaturas quentes e invernos amenos); (2) modelos de evolução simples de taxa constante fornecem uma representação pobre sobre como os nichos climáticos evoluem; (3) a reconstrução ancestral de caracteres indicou claramente que todos os clados tiveram evolução dos nichos climáticos mais pronunciada perto do presente, particularmente nos últimos 10 milhões de anos; (4) a evolução do nicho climático dos primatas foi caracterizada por considerável heterotaquia, dada a pouca adequabilidade dos modelos de evolução simples e pela detecção de múltiplas mudanças das taxas de evolução, e (5) as mudanças nas taxas de evolução ocorreram repetidamente e independentemente em diversas linhagens e eixos do nicho, com acelerações sendo mais frequentes que desacelerações.

Este estudo revela características novas e importantes para a compreensão da evolução dos nichos climáticos, podendo ser de interesse geral para os estudos comparativos. As perguntas que guiaram este estudo, assim como os métodos empregados, podem ser aplicados para qualquer grupo de organismos para o qual tenha-se dados de distribuição geográfica e informações sobre as preferências climáticas de cada espécie, além de suas relações filogenéticas. Vale ressaltar que, quanto maior o conjunto de dados e maior o número de espécies presentes na filogenia, mais precisas serão as inferências sobre os resultados. Ainda, avaliar os

resultados deste estudo em função de diferentes organismos trará contribuições fundamentais para os estudos de evolução de nicho, identificando se o padrão encontrado em primatas é comum a outros grupos ou se a evolução de nicho é idiossincrática.

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Tempo and mode of climatic niche evolution in Primates

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Climatic niches have increasingly become a nexus in our understanding of a variety of ecological and evolutionary phenomena, from species distributions to latitudinal diversity gradients. Despite the increasing availability of comprehensive datasets on species ranges, phylogenetic histories, and georeferenced environmental conditions, studies on the evolution of climate niches have only begun to understand how niches evolve over evolutionary timescales. Here, using primates as a model system, we integrate recently developed phylogenetic comparative methods, species distribution patterns, and climatic data to explore primate climatic niche evolution, both among clades and over time. In general, we found that simple, constant-rate models provide a poor representation of how climatic niches evolve. For instance, there have been shifts in the rate of climatic niche evolution in several independent clades, particularly in response to the increasingly cooler climates of the past 10 My. Interestingly, rate accelerations greatly outnumbered rate decelerations. These results highlight the importance of considering more realistic evolutionary models that allow for the detection of heterogeneity in the tempo and mode of climatic niche evolution, as well as to infer possible constraining factors for species distributions in geographical space.

KEY WORDS: **Catarrhini, macroevolution, phylogenetic comparative methods, rate heterogeneity, Strepsirrhini, Platyrrhini.**

Climatic niches—the set of environmental conditions associated with the occurrence of a given species (Grinnellian niche—Soberón 2007)—have become a central concept in ecology and biogeography in recent years (Pearman et al. 2008; Wiens et al. 2010). For instance, although current patterns of species distributions are ultimately determined by three main mechanisms, namely speciation, extinction, and dispersal (Ricklefs 1987; Wiens and Donoghue 2004; Mittelbach et al. 2007), each of these mechanisms can in turn be strongly affected by climatic conditions, such as temperature and precipitation (Woodward and Kelly 2003; Fleagle and Gilbert 2006; Hua and Wiens 2013; see also Hawkins et al. 2003; Currie et al. 2004; Lomolino et al. 2010; Gavilanez and Stevens 2012; Pyron and Wiens 2013; Smith 2013). This has led to several studies describing the general properties of climatic niches in a variety of taxa (e.g., Hof et al. 2010; Jakob et al. 2010; Kamilar and Muldoon 2010; Cooper et al. 2011; Olalla-Tárraga et al. 2011; Araújo et al. 2013; Bonetti and Wiens 2014). However, our understanding of the tempo and mode of evolution (Simpson 1944) in the case of climatic niches is still incipient, particularly using comprehensive interspecific datasets.

Studies to date on the evolution of climatic niches have primarily focused on two main areas: assessing phylogenetic signal and niche conservatism (e.g., Peterson et al. 1999; Losos 2008; Revell et al. 2008; Wiens 2008; Crisp et al. 2009; Buckley et al. 2010; Dormann et al. 2010; Hof et al. 2010; Wiens et al. 2010; Cooper et al. 2011; Olalla-Tárraga et al. 2011; Peterson 2011; DeSantis et al. 2012; Münkemüller et al. 2012, 2015; Duran et al. 2013; Kamilar and Cooper 2013) and measuring the relative fit of simple models of trait evolution, such as Brownian motion (BM, Felsenstein 1973, 1985) and Ornstein–Uhlenbeck (OU, Hansen 1997). The latter application has been instrumental to uncover several important aspects of niche evolution, such as its relation

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to species diversification (Kozak and Wiens 2010a,b; Schnitzler et al. 2012; Machac et al. 2013; Lawson and Weir 2014), the conditions favoring niche divergence (e.g., Evans et al. 2009; Kozak and Wiens 2010a), and the extent to which different climatic niche axes might evolve according to distinct dynamics (e.g., Kamilar and Muldoon 2010; Cooper et al. 2011; Duran et al. 2013). However, there has been increasing concern over whether such simple, time-homogeneous models of trait evolution are able to properly describe trait evolution along actual phylogenetic histories (Freckleton and Harvey 2006; Eastman et al. 2011; Thomas and Freckleton 2011; O'Meara 2012; Pennell et al. 2015). Indeed, the most likely model among a set of poor models is still a poor model, and the extent of misspecification in commonly applied models of trait evolution is still poorly known. Alternatives to time-homogeneous models involve the possibility of testing for shifts in the rates of trait evolution, both over time (early burst [EB], Harmon et al. 2010; delta, Pagel 1999) and among clades (O'Meara et al. 2006; Thomas et al. 2006; Revell et al. 2011). A common limitation of some models that allow for shifts in rates of evolution in different parts of a tree is the need to specify beforehand the position of such shifts (O'Meara 2012). This limitation has been mitigated by methods that allowed for a posteriori location of rate shifts, such as Accommodating Uncertainty in Trait Evolution Using R (AUTEUR, Eastman et al. 2011, see also Venditti et al. 2011) and Models of Trait Macroevolution on Trees (MOTMOT, Thomas and Freckleton 2011; see also Revell et al. 2011; Ingram and Mahler 2013; and Uyeda and Harmon 2014 for additional alternatives). Both methods have been used in several studies looking at variation in the evolution of morphological traits (e.g., Anderson et al. 2013; Davies et al. 2013; Garcia-Porta and Ord 2013; Pie and Tschá 2013; Rabosky et al. 2013), yet similar studies on other types of characters, such as climatic niches, are still scarce (but see Smith and Beaulieu 2009; Litsios et al. 2012).

In this study, we combined information on the phylogenetic relationships, climatic data, and phylogenetic comparative methods to provide the most comprehensive study of climatic niches to date. We used the order Primates as our model system, given that they are unparalleled among most taxa with respect to the level of detail in the knowledge about their distribution and phylogenetic relationships (Lehman and Fleagle 2006; Springer et al. 2012). First, we used principal component analysis (PCA) to determine the main axes of variation in climatic niches of 334 primate species. The absolute fit of scores on different principal components (PCs) to several simple models of trait evolution was assessed using posterior predictive simulation, which showed strong evidence for heterogeneity in rates of climatic niche evolution. Such heterogeneity was further explored using methods that quantified variation in rates both over time and among lineages. In particular, our results indicate several independent shifts in rates of climatic niche evolution, especially over the past 10 My, possibly in association with the period of climatic cooling that took place during the late Miocene.

Methods

DATA COLLECTION

To characterize the evolution of primate climatic niches, we compiled an extensive dataset that included all species for which we could simultaneously obtain information on phylogenetic, distribution, and climatic data. Phylogenetic relationships and divergence times among primate species were obtained from Springer et al. (2012), which is the most complete primate molecular phylogeny to date. Shapefiles of distribution maps were downloaded from the International Union for Conservation of Nature database (IUCN 2012), from which only shapefiles from extant and probably extant species in their native range were retained for later analysis. The final dataset comprised 334 species and included the suborder Strepsirrhini (105 species) and the infraorders Catarrhini (138 species), and Platyrrhini (91 species), representing around 70% of the currently recognized primate species (Mittermeier et al. 2013).

The climatic niche of each species was characterized using data on temperature, precipitation, and altitude obtained from WorldClim 1.4 (Hijmans et al. 2005). This dataset consists of 19 bioclimatic variables and altitude, with a spatial resolution of 2.5' ($\approx$5 km). The mean values for each variable across the entire range of each species were obtained and manipulated using the packages raster 2.2-31 (Hijmans 2014), rgdal 0.9-1 (Bivand et al. 2014), maptools 0.8-30 (Bivand and Lewin-Koh 2014), and plyr 1.8.1 (Wickham 2014). All analyses in this study were carried out in R 3.0.3 (R Development Core Team 2014). The final dataset with all studied species and their respective mean values from each of the 20 variables is available as supplementary material (Table S1).

DATA ANALYSIS

Raw data were first transformed into *z*-scores and then subject to a PCA based on their covariance matrix. We transformed the original data into *z*-scores prior to the PCA given that the vast differences in measurement scales between temperature and precipitation could severely bias the obtained results. This type of approach has been a common practice in studies on the evolution of climatic niches to deal with multicollinearity and to reduce the dimensionality in the studied datasets (e.g., Broennimann et al. 2007; Kamilar and Muldoon 2010; Kozak and Wiens 2010a; Duran et al. 2013). However, it has been recently shown that fitting models of evolution to PCA scores might lead to an artifactual support for reconstructing more variation early in the history of a clade (Uyeda et al. 2015). We addressed this issue by repeating our analyses using a version of the PCA that takes into account the phylogenetic structure of the data when computing the PCA

Table 1. Loadings of a principal components analysis of primate climatic niches.

Variables	PC1	PC2	PC3
Altitude	−0.24	0.22	−0.12
Annual mean temperature	0.28	−0.23	0.02
Mean diurnal	−0.14	−0.25	−0.16
Isothermality	0.26	0.11	−0.25
Temperature seasonality	−0.27	−0.03	0.18
Maximum temperature of warmest month	0.15	−0.38	0.04
Minimum temperature of coldest month	0.32	−0.06	−0.06
Temperature annual range	−0.27	−0.17	0.09
Mean temperature of wettest quarter	0.20	−0.28	0.16
Mean temperature of driest quarter	0.30	−0.14	−0.08
Mean temperature of warmest quarter	0.20	−0.32	0.12
Mean temperature of coldest quarter	0.30	−0.14	−0.07
Annual precipitation	0.22	0.27	0.23
Precipitation of wettest month	0.10	0.05	0.52
Precipitation of driest month	0.20	0.29	−0.05
Precipitation seasonality	−0.17	−0.30	0.23
Precipitation of wettest quarter	0.12	0.10	0.52
Precipitation of driest quarter	0.21	0.30	−0.06
Precipitation of warmest quarter	−0.04	0.20	0.39
Precipitation of coldest quarter	0.23	0.19	−0.03
Standard deviation	3.07	2.14	1.65
Proportion of variance	0.47	0.23	0.14
Cumulative proportion	0.47	0.70	0.84

The first three principal components were selected based on the broken-stick criterion.

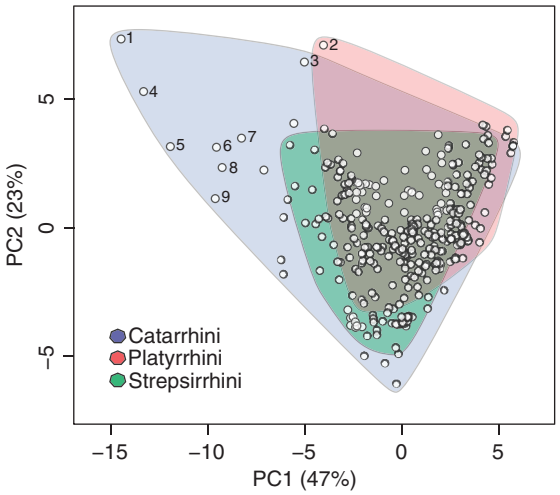

Figure 1. Scores along the first two PC axes representing the climatic niche space of primate species. Each data point represents the mean score for a given species. The numbered points represent species that occupy extreme regions the climatic niche space: (1) *Rhinopithecus bieti*, (2) *Aotus lemurinus*, (3) *Gorilla beringei*, (4) *Macaca munzala*, (5) *R. roxellana*, (6) *R. brelichi*, (7) *M. fuscata*, (8) *M. thibetana*, and (9) *M. sylvanus*. Low score values in PC1 indicate lower temperatures, particularly in coldest months, whereas high score values in PC2 indicate colder climatic conditions, with low mean temperatures during warmest months.

(Revell 2009), as implemented in PHYTOOLS 0.4-45 (Revell 2012). However, given that the PC scores and loadings from both analyses were highly correlated ($r > 0.98$), the results of the phylogenetically corrected PCA will not be shown for the sake of brevity. The PCA axes retained for later analysis were selected according to the broken-stick criterion (Jackson 1993) using VEGAN 2.0-10 (Oksanen et al. 2013). As a first approximation, to investigate the evolution along each climatic niche axis, we fit three alternative models of evolution to the scores from each of the selected PC axes: (1) the BM model, in which traits evolve as a random walk process where the trait change follows a constant rate and is nondirectional and their magnitude is independent of current or past states through time (Felsenstein 1985); (2) OU model, which tests the scenario of stabilizing selection with a single adaptive peak (Hansen 1997; Butler and King 2004); and (3) the EB model, in which the rate of trait evolution can be accelerated during the early stages of the history of a given clade (Blomberg et al. 2003; Harmon et al. 2010). Model fit using the Akaike Information Criterion (AIC, Akaike 1973) was calculated using GEIGER 2.0.3 (Pennell et al. 2014a).

The level of adequacy of the tested models was assessed using posterior predictive simulation (also known as parametric bootstrapping), as implemented in ARBUTUS 1.1 (Pennell et al. 2014b). In brief, the best-fit model, as indicated by the lowest AIC value in previous analyses, was matched with the trait data

and used to create a unit tree. This unit tree is a transformation of the original phylogenetic tree, which is molded to capture the evolutionary dynamics with which a particular trait evolves according to the selected model. Based on this unit tree, we simulated 10,000 datasets using the estimated parameters. A series of test statistics were then calculated in both the original and each of the simulated datasets. If the model is an adequate description of the original dataset, the observed test statistic should fall within the distribution of the corresponding statistic of the simulated datasets, whereas potential discrepancies could indicate that the chosen model does not capture specific properties of the original dataset. The used test statistics were: M_{SIG} is the mean of squared independent contrasts and refers to the measure of the overall evolutionary rate; C_{VAR} is the coefficient of variation for the absolute contrasts and identifies whether the rate heterogeneity is being assumed properly by the evolutionary model; S_{VAR} and S_{ASR} are based on estimates of slopes from fitting the linear model of the absolute contrasts values with the expected variances, and with the inferred ancestral state at a given node, respectively. The former allows for testing if the evolutionary rates are related with the branch lengths, whereas the latter is used to test whether the rates are related with the trait values; S_{HGT} measures the slope of a linear model of the absolute contrast values against the height of the node to evaluate its variation with respect to time; finally, the D_{CDF} which uses the *D*-statistic to compare if the distribution of the independent contrasts follows the normal distribution, as expected for the contrasts under BM (Pennell et al. 2015). It is important to note that the tested statistics were not used during the simulation themselves, such that their comparison would reveal specific ways in which the empirical dataset varies from expectations based on simple models of evolution.

We investigated variation in rates of climatic niche evolution using methods that assess changes both over time and among lineages. Temporal variation in climatic niche evolution was studied using the *phenogram* function in PHYTOOLS 0.4-45 (Revell 2012), where the phylogeny is plotted such that the position of each node on the y-axis corresponds to the maximum likelihood estimate of the corresponding ancestral state. In addition, we investigated variation in climatic niche evolution among lineages using AUTEUR (Eastman et al. 2011), as implemented in the AUTEUR package 0.12.0118 (Eastman et al. 2011). This method performs a Bayesian analysis using the reversible jump Markov chain Monte Carlo, which allows the determination of the number, location, and direction of the shifts on a given phylogeny by comparing models with different numbers of evolutionary rates (Eastman et al. 2011). Each AUTEUR analysis was run for 10,000,000 generations, with chain sampling every 1000 generations, and repeated twice to ensure convergence. We compared the obtained results with a second approach called MOTMOT (Thomas and Freckleton 2011). Although these two methods share the property of not requiring the specification of the number and position of potential shifts beforehand, they differ considerably in their statistical approaches, such that a comparison of their results should provide a more robust inference regarding variation in rates of climatic niche evolution among lineages. However, given their considerable overlap in their objectives, we only present the MOTMOT analysis as supplementary material (Fig. S1).

Results

The loadings from the PCA of primate climatic niches are shown in Table 1. The PCA was efficient in summarizing the main trends in the dataset, given that the first three PCs selected according to the broken-stick criterion accounted for 84% of the variance in the dataset (Table 1). The first PC reflected variation in temperature, particularly during the coldest/driest months, whereas the second PC indicated a negative relationship between temperature and precipitation, particularly during the warmest months. Finally, the third PC reflected mostly variation in precipitation, especially during the warmest/wettest months (Table 1). Interestingly, the distributions of each of the three primate clades on the PCA ordination plot were highly congruent, with most species being found in conditions of warm temperatures and mild winters (Fig. 1). Catarrhini showed considerably broader climatic niches in relation to other clades, particularly on the first PC, which reflects their distribution into regions with colder temperatures and more pronounced seasonality (Fig. 1).

A comparison of model fit based on AIC indicated that OU was the best-fit model of trait evolution for all three PCs (Table 2). However, analyses of absolute fit based on posterior predictive simulation indicated an overall poor adequacy of the OU model to the data, particularly because they do not account for variation in rates of evolution (Fig. 2). Significant departures from the simulated statistics were common, particularly with respect to C_{VAR}, S_{VAR}, and S_{ASR} (Fig. 2). Moreover, the direction of bias also varied among clades, with alternating patterns of statistics being higher or lower than expected (Fig. 2). In general, these results are consistent with substantial variation in rates in the analyzed datasets (heterotachy), suggesting that the interpretation of simple models that assume constant rates across the entire phylogeny might be misleading.

When variation in rates through time was assessed based on the reconstruction of ancestral states, a consistent pattern was uncovered indicating an apparent late increase in the rate of evolution of climatic niches, particularly during the past 10 My, most notably for catarrhines (Fig. 3) Interestingly, the lineages occupying distinct regions of climatic space, as indicated in Figure 1, seem to have occupied these regions fairly recently (Fig. 3). Likewise, AUTEUR analyses detected frequent shifts in rates of climatic niche evolution among lineages (Figs. 4 and S2, see also Fig. S1

Table 2. Fit of the macroevolutionary models with respect to primate climatic niche axes.

		Brownian motion (BM)	Ornstein–Uhlenbeck (OU)	Early burst (EB)
PC1	logL	−849.14	−794.35	−849.14
	AIC	1702.31	**1594.76**	1704.35
	α		20.61	
	a			0
PC2	logL	−779.6	−702.25	−779.6
	AIC	1563.25	**1410.56**	1565.28
	α		31.73	
	a			0
PC3	logL	−698.37	−607.28	−698.37
	AIC	1400.77	**1220.62**	1402.81
	α		36.94	
	a			0

Bold values indicate the lowest AIC estimates for each PC among the tested models.

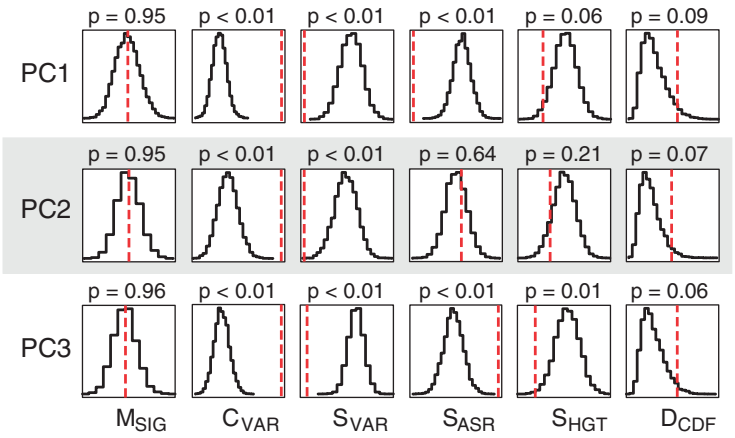

Figure 2. Distribution of test statistics based on posterior predictive simulation of three PC scores of primate climatic niches (black lines), observed statistics (dashed red lines), and their respective *P*-values. See text for more details about each statistic.

for the corresponding analysis using MOTMOT). Regardless of the niche axis, most lineages shared a similar background rate of climatic niche evolution, with many shifts distributed throughout the phylogeny involving few species in relatively recent nodes, such as *Piliocolobus gordonorum, P. kirkii, P. rufomitratus, P. tephrosceles, and P. foai* on PC1 or the *Rungwecebus kipunji* on PC2, and *Trachypithecus geei* and *T. johnii* on PC3 (Figs. 4 and S2). Interestingly, lineages that show rate shifts in PC1 are different from those showing rate shifts on PC2. Finally, the vast majority of the identified shifts involved rate increases (Figs. 4 and S2), suggesting that decreases in rates of climatic niche evolution of primates are rare, with only two cases of rate decrease across all analyses on PC1 and PC2. The first included the entire infraorder Lemuriformes (Strepsirrhini) in PC1, but the support for this specific shift rate was low based on the AUTEUR method (Fig. 4). The other rate decrease was observed in some of the species of *Macaca*, in the Catarrhini clade, but in this case with strong support. Coincidently, both of these instances occurred with species that live in islands (Madagascar in Africa and the Sulawesi in Indonesia, respectively). In general, the greatest number of rate shifts was detected in Catarrhini, with strong support for rate shifts in all the three PCs. These shifts were detected in lineages from southern and southeastern from Asia, and in species from Africa. Only one case of shift rate with strong support occurred in South America, comprising species of *Leontopithecus* (Fig. S3).

Discussion

The results of the present study provide a comprehensive view of how climatic niches evolved over the course of the history of Primates. First, the occupation of climatic space was not homogeneous among primate lineages, with most species being concentrated under relatively mesic conditions (i.e., warm temperatures and mild winters—Fig. 1 and Table 1). In addition, primate climatic niche evolution was characterized by considerable heterotachy, given the low adequacy of simple models of evolution

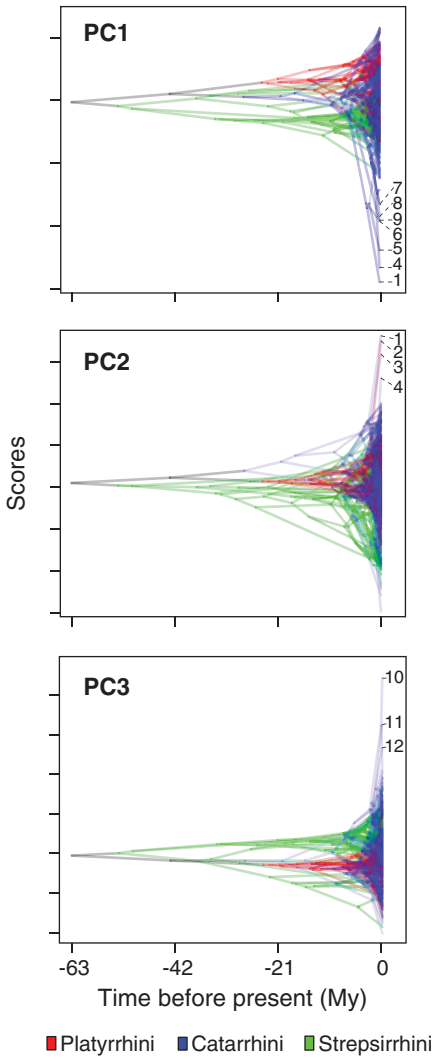

Figure 3. Reconstruction of ancestral states along primate climatic niche axes. The position along the x-axis corresponds to the node age in millions of years and the y-axis positions correspond to the reconstructed character value based on PC scores. Each of the three clades is distinguished by colors indicated in the legend. Catarrhini, in blue, shows the broadest variation in climatic niche occupation in all three PCA axes. The number in divergent branches corresponds to the species indicated in Figure 1, following the same order from that legend, with three additional species in PC3: (10) *Trachypithecus geei*, (11) *Macaca silenus*, and (12) *T. laotum*.

(Fig. 2) and the detection of multiple rate shifts (Fig. 4). Finally, even though these shifts occurred independently in several lineages and niche axes, they tended to be more frequent near the present (Fig. 3). It is noteworthy that ancestral character reconstructions clearly show that all clades showed more pronounced evolution of climatic niches near the present, particularly in past 10 My (Fig. 3). Despite the inherent uncertainties surrounding the reconstruction of ancestral characters (Schluter et al. 1997), the consistent pattern in different clades, which live across geographically distinct locations, suggests that this pattern is robust, particularly in the case of Catarrhini. Results based on paleoclimatic and paleovegetational data suggest severe climatic changes in the globe over the past 65 My, including glacial and interglacial cycles (e.g., Zachos et al. 2001). In particular, the period from approximately 23 to 5 My, comprising the Miocene period, included several anomalous cooling phases characterized by shorter periods of smaller glaciations (Zachos et al. 2001). These observations match our results, suggesting that the diversification of the primate climatic niches could be a consequence of Earth's cooling in this period. Interestingly, lineage diversification itself seems to have been accelerated over the past ≈7 My (see Fig. 8 in Springer et al. 2012), suggesting a possible causal relationship between both rates, as suggested for salamanders (Kozak and Wiens 2010a). Changes in vegetation during the Miocene are also thought to be related with the global cooling (Briggs 1995; Dutton and Barron 1997). Together with paleoclimatic variation, the vegetational changes seem to correlate with the diversification of primates climatic niches in the present study, particularly given the importance of forest architecture to primate community structure and richness (Gouveia et al. 2014). The biogeographic history from Platyrrhini, for instance, suggests that this neotropical clade evolved in South America for more than 26 My and experienced changes in fauna, continent structure, climate, and flora, with the Amazonian rain forest starting to reach its current configuration at about 15 My (Rosenberger et al. 2009). Similarly, the catarrhine family Cercopithecidae arose in early Miocene (Briggs 1995) and their diversification also seems to be related with changes in their climatic niches, particularly in the case of *Macaca* and *Trachypithecus* (see Fig. 3). Moreover, the relatively distinctive evolutionary patterns found in SE Asian primates are also reflected in their correlates of species richness, which seem to be more associated with precipitation than other primate lineages (Gouveia et al. 2014).

The extensive variation in rates of climatic niche evolution among the primate lineages (see Fig. 4) generally occurred near the present, in agreement with the results discussed above. Interestingly, there was quantitative variation in the magnitude of the shifts among primate clades. Catarrhini shows more frequent changes in evolutionary rates (Fig. 4) and the climatic niche divergence in this clade was markedly higher (Fig. 3). On the other hand, shifts in Platyrrhini and Strepsirrhini were less severe despite their substantial lineage diversification, suggesting that, for these clades, species diversification and the climatic niche evolution were at least partially uncoupled. It is important to acknowledge that error in PC scores could potentially contribute to the observed pattern of recent shifts in rates of climatic niche evolution, given that they would falsely imply that the niches of the involved species would have experienced a severe change in their

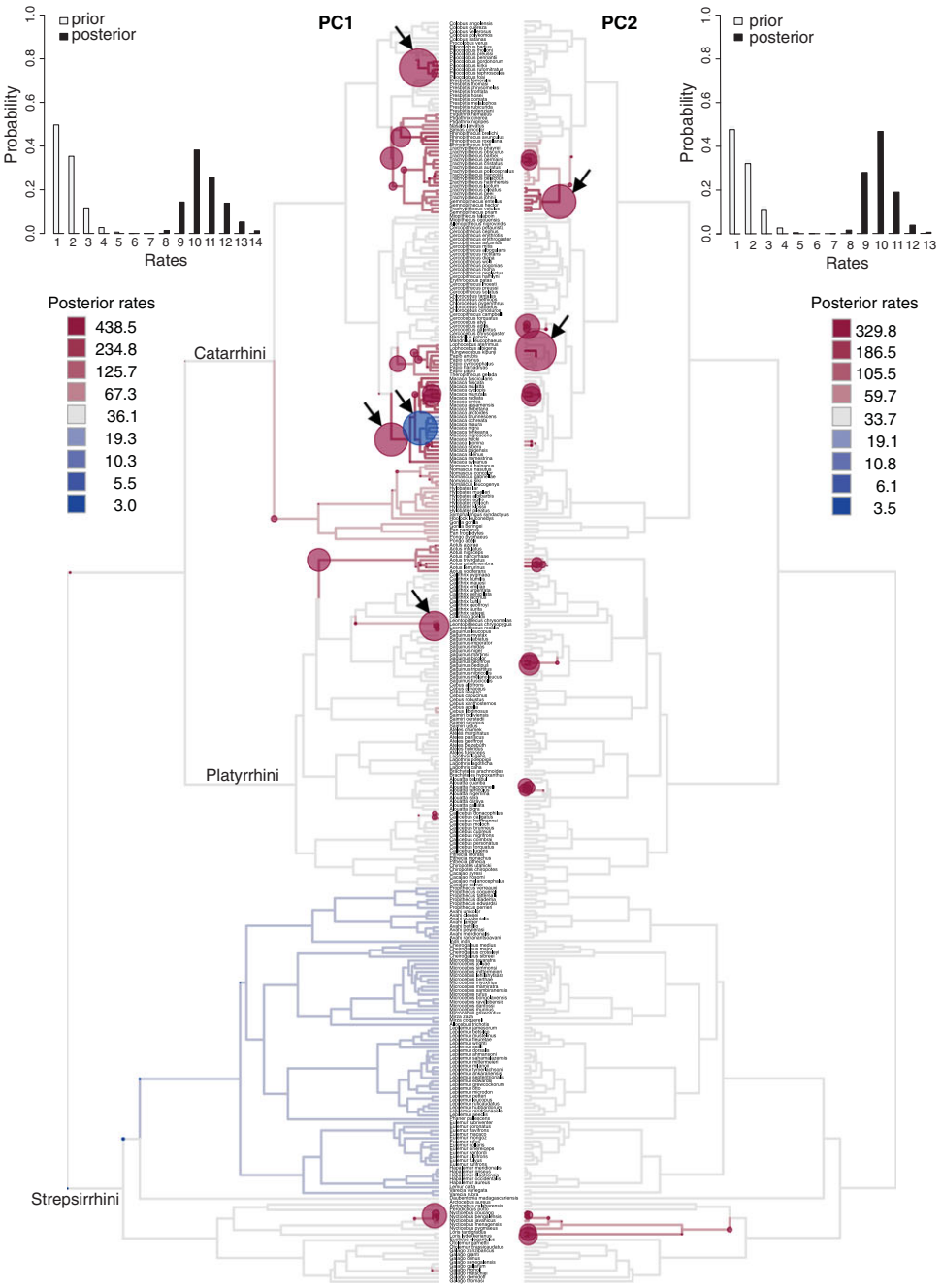

Figure 4. **Posterior rate estimates of primate climatic niche evolution based on the AUTEUR method, indicating how the shift rates varied across the phylogeny. Background rates are shaded in gray, whereas background deviating rates are shaded in darker colors according to the posterior rates in the legend. Circles correspond to level of the support for each shift. We added arrows to indicate rate shifts with the strongest support. Interestingly, all species indicated in Figures 1 and 3 are shown here as experiencing shifts in rates of climatic niche evolution.**

recent evolutionary past in comparison with its closely related species. However, we believe that this effect is not capable of producing the results obtained in our study given that the vast majority of the detected shifts were not reconstructed on terminal branches (as one would expect in the case of measurement error on a single species). In addition, the consistency in terms of timing and geographical distribution of the involved species is strongly suggestive of a real biological mechanism underlying those shifts.

A suggestive pattern presented with our analysis is the observation that several of the lineages with significant rate shifts have their geographic distribution related to mountain ranges (Fig. S3). Examples include the catarrhine *Macaca sylvanus*, which lives in

the Atlas Mountains in northwestern Africa, the *R. kipunji*, which has a very restricted distribution in Udzungwa and Livingstone Mountains in southern Tanzania, and the primate species from southern and southeastern Asia, which may be influenced by the mountain range of the Himalayas (Fig. S3). One could hypothesize that these changes in evolutionary rates could be linked to different climatic conditions and gradients in these regions. An intriguing finding related to these mountainous environments and with the changes in evolutionary rates is that the species presented in Figure S3 inhabit regions strongly influenced by the monsoon systems, except for the South America species. The two strongest monsoons on Earth occur in the Asian-Australian system and in western Africa (Trenberth et al. 2000) and are strongly related with the Himalayas mountain ranges (Webster et al. 1998). India, for instance, has the monsoons as the major weather phenomenon (Overpeck et al. 1996), and all the primates include in our analyses that occur in this region exhibit rate shift in climatic niche evolution.

Although there is increasing evidence for a crucial role of climatic conditions in determining mammal species distributions and their fluctuations over time (e.g., Smith 2013), it is important to recognize that other factors, such as dispersal capacity (Siefert et al. 2015) and biotic interactions (Holt and Barfield 2009) might play an important role in determining geographical range limits. The extent to which these factors drive primate distributions is still poorly understood, yet their recognition does not contradict the results of our study. In particular, our analyses are based on the climatic conditions actually experienced by different species throughout their entire range. Such conditions could either directly affect the physiological tolerance of a given species or indirectly impact the strength of its biotic interactions, and we are agnostic with respect to the relative importance of these potential direct and indirect effects. As a consequence, climatic and biotic drivers of geographical distributions do not represent mutually exclusive mechanisms, yet understanding their interplay over the course of the evolutionary history of a clade is a major challenge for future studies.

This study underscores the potential of recently developed phylogenetic comparative methods in uncovering complex dynamics in the evolution of climatic niches. Many studies, particularly in the context of environmental niche modeling, tend to assume that climatic niches are static, yet little is known about how niches evolve when that assumption is not met (Pearman et al. 2008). In this study, we demonstrate extensive heterotachy in evolutionary rates in primate climatic niches, revealing the location, number and direction of changes in rates in lineages and the differences among clades. In addition, many models commonly used in studies of character evolution showed poor absolute fit to our dataset, deviating in several ways from the general statistics investigated through posterior predictive simulation. This suggests that more realistic evolutionary models must be considered to better describe the evolutionary pattern of climatic niche evolution in primates. We raised several important points that should be investigated carefully in future studies, such the suggested relationship between the rate shifts with the mountain ranges and monsoons systems, which should also be explored for different taxa. Finally, we showed how the rate of climatic niche evolution can be affected by global-scale changes in world climate, particularly over the past 10 My, providing important expectations for future studies on other model systems.

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Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's website:

Table S1. Raw data from the 334 primate species with their respective mean values for the 20 variables used in PCA analysis.
Figure S1. Shifts in rates of climatic niche evolution along the first three PC scores, based on the Models of Trait Macroevolution on Trees (MOTMOT; Thomas and Freckleton 2011) method, as implemented in motmot package 1.0.1 (Thomas and Freckleton 2011).
Figure S2. Posterior rate estimates of climatic niche evolution along the third PC, based on the AUTEUR method, indicating how the shift rates varied across the phylogeny.
Figure S3. Geographical distribution of the species with high support rate shifts showed in AUTEUR analysis in Figure 4.